Aspects of the biology of three exploited deepwater sharks *Centrophorus squamosus, Centroscymnus coelolepis* and *Deania calceus* (Elasmobranchii: Squalidae) from the continental slopes of the Rockall Trough and Porcupine Bank

A thesis presented to the
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By

Maurice Clarke B.A. (Mod.)

Head of Department:
Professor Eamon J. Duke

Department of Zoology,
University College,
Belfield,
Dublin 4

Supervisors:
Professor John J. Bracken

Department of Zoology,
University College,
Belfield,
Dublin 4.

Dr. Paul L. Connolly
Divisional Director

Marine Institute,
Marine Fisheries Services Division,
Abbotstown,
Dublin 15.

October 2000

This work is dedicated to my parents

Declaration

I hereby declare that I am the sole author of this work, now submitted in fulfilment of the thesis requirement for the degree of Doctor of Philosophy of the National University of Ireland. I also certify that the material in this thesis has not already been accepted for any other degree and is not being submitted for any other degree.

Signed _____

Maurice Clarke

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Contents

Abstract

Aspects of the biology of three exploited sharks (Elasmobranchii: Squalidae) from the continental slopes of the Rockall Trough and Porcupine Bank (NE Atlantic) were examined using specimens taken during trawl and long-line surveys (December 1995 to December 1999) and commercial samples obtained from trawlers (March 1997 to June 1998). The species under study were *Centroscymnus coelolepis, Centrophorus squamosus*, and *Deania calceus*. The entire depth range (300 m – 1,800 m) of each species was sampled. *C. squamosus* and *D. calceus* were abundant between 700 m and 900 m. *C. coelolepis* was more abundant deeper (1,300 m) but gravid females were more abundant in shallower waters. Small specimens of each species were absent from the study area. Trawls and long-lines selected for different size ranges of *C. coelolepis* and *D. calceus*, though not *C. squamosus*. Deepwater bobbin and French high headline trawls did not select for different size ranges of *C. coelolepis*. Unlike the other species *D. calceus* is not landed. Discard rates from long-liners exceeded 40 % of total catch depending on depth fished. While percentage discard rates from trawlers were lower, an estimated 745 t of this species were discarded in 1996 alone. Sexual maturity was achieved at large size, more than 75 % of maximum length in each species. No evidence of seasonal cycles in reproduction was found from spermatogenic analysis or the occurrence of maturity stages. Mean ovarian fecundity was low; *C. squamosus*, 8, *C. coelolepis* and *D. calceus* 13. Dorsal spine sections were used for age estimation. Significant positive regressions of spine width and total length were found and the growth rates of first and second spines were not significantly different. Estimates of 21-70 years (*C. squamosus*) and 11-35 years (*D. calceus*) were obtained. Agreement within 1 year was found for more than 93 % of *D. calceus* and 88 % of *C. squamosus* first and second spines. Empirical and von Bertalanffy growth data suggest that growth had slowed down or ceased before the onset of maturity. Estimates of natural mortality (M) for *C. squamosus* (0.066 – 0.087) and *D. calceus* (0.116-0.177) were low. Fishing mortality (F) for *D. calceus* was estimated to have reached the level of M for females but below M for males. This study suggests that these species have conservative life-history strategies. No management plan currently exists for the multi-species deepwater fishery in the northeast Atlantic. In the absence of suitable abundance indices, stock assessment should be based on known life history parameters of target and by-catch species. Such an approach will facilitate the rational management of the fishery.

Aspects de la biologie de trois requins profonds, *Centrophorus squamosus*, *Centroscymnus coelolepis* et *Deania calceus* (Elasmobranchii: Squalidae) du talus continental du Fossé de Rockall et du Banc de Porcupine

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par

Maurice Clarke

Soutenue le 8 décembre 2000 devant le Jury:

Professor John Bracken	Président
Professor Kazunari Yano	Rapporteur
Dr. Tom Hayden	Rapporteur
Dr. Paul Connolly	Examinateur

Correspondance à: Maurice Clarke, Marine Institute, Abbotstown, Dublin 15, République d'Irlande.
Tel: 00353 1 8228202, Fax: 00353 1 8205078, E-mail: maurice.clarke@marine.ie,
www.marine.ie/library/publications.html-ssi

RESUMÉ

Divers aspects de la biologie de trois requins (Elasmobranchii: Squalidae) habituellement exploités par la pêche sur le talus continental du Fossé de Rockall et du Banc de Porcupine (Atlantique NE) ont été examinés à partir de spécimens collectés lors de campagnes scientifiques au chalut ou à la palangre (décembre 1995 à décembre 1999), ainsi qu'à partir d'échantillonnages des débarquements des chalutiers commerciaux (mars 1997 à juin 1998). Trois espèces ont été étudiées : *Centroscymnus coelolepis*, *Centrophorus squamosus*, et *Deania calceus*, les observations recouvrent leur répartition bathymétrique habituelle (300 m – 1 800 m). Dans cette gamme de profondeur, *C. squamosus* et *D. calceus* étaient plus abondants entre 700 m et 900 m tandis que *C. coelolepis* l'était par plus grande profondeur (1 300 m). Les femelles gravides étaient plus abondantes dans les eaux moins profondes mais il n'a pas été capturé de petit individu d'aucune espèce. Les *C. coelolepis* pêchés par les chaluts commerciaux irlandais et français avaient des tailles significativement différentes. Contrairement aux deux autres espèces, *D. calceus* n'est pas commercialisé actuellement, il constitue cependant plus de 40 % de la capture en poids de la pêche à la palangre. Dans les chaluts, ce pourcentage est inférieur, on estime néanmoins que 745 t ont été capturées en 1996. La maturité sexuelle des trois espèces est atteinte à une taille relativement importante, soit plus de 75 % de la taille maximale. Les analyses spermatogénetiques ainsi que les stades de maturité sexuelle ne montrent pas de cycle saisonnier de reproduction. Les taux de fécondité sont bas : 8 embryons par femelle chez *C. squamosus*, et 13 chez *C. coelolepis* et *D. calceus*. Des estimations d'âge ont été réalisées sur des sections des épines dorsales. Des régressions significativement positives entre le diamètre des épines et de la longueur totale de l'animal ont été trouvées et les taux de croissance de la première et de la deuxième épine ne sont pas significativement différents. Des estimations d'âge de 21-70 ans (*C. squamosus*) et 11-35 ans (*D. calceus*) ont été obtenues. Respectivement 93 % et 88 % des estimations basées sur les première et deuxième épines dorsales ne différaient pas de plus d'un an pour *D. calceus* et *C. squamosus*. Certaines données empiriques et les paramètres du modèle de von Bertalanffy indiquent que la croissance diminue ou s'arrête totalement avant le début de la maturité sexuelle. Les estimations des mortalités naturelles (M) pour *C. squamosus* (0,066 – 0,087) et *D. calceus* (0,116 – 0,177) sont basses. Cette étude suggère que ces espèces ont des stratégies de vie sensibles à l'exploitation. En absence d'indices d'abondance convenables, l'évaluation des stocks devrait être basée sur les paramètres connus des stratégies de vie des espèces. Une telle approche faciliterait la gestion rationnelle de la pêche.

Correspondance à: Maurice Clarke, Marine Institute, Abbotstown, Dublin 15, République d'Irlande.
Tel: 00353 1 8228202, Fax: 00353 1 8205078, E-mail: maurice.clarke@marine.ie,
www.marine.ie/library/publications.html-ssi

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1. Introduction

The deepwater environment is generally considered to comprise waters of greater than 400 metres. Though some pelagic sharks may descend to these depths on occasion, the term deepwater shark is generally used to describe demersal forms. However the definition is not a taxonomic one as several separate groups of elasmobranchs are well represented in deep waters (Merrett and Haedrich, 1997). Among these taxa, the Squalidae have reached their greatest diversity in this environment. These are a diverse group of small to very large sharks, with cylindrical bodies and small dorsal fins with or without fin spines (Compagno, 1984). Despite the paucity of scientific information on the Squalidae they are heavily exploited in many fisheries worldwide (Gordon, 1999). Those "poorly known, slow growing dog-fishes" described by Compagno (1990) as caught in "offshore, deep-trawling operations by international fleets and local long-line fisheries" are considered to be at considerable risk. Such fisheries exist west and north of Ireland, in the deep waters of the Rockall Trough and the continental slopes of the Porcupine Bank.

At least eleven Squalid deepwater sharks are regularly caught in the waters west and north of Ireland (Gordon and Swan, 1997). However only two, Portuguese dogfish *Centroscymnus coelolepis* and leafscale gulper shark *Centrophorus squamosus* are landed (Charuau *et al.* 1995). The livers of others, such as birdbeak dogfish *Deania calceus*, kitefin shark *Dalatias licha* and greater lantern shark *Etmopterus princeps* (Iglesias and Paz, 1995) are sometimes retained, but the carcasses are discarded. These fisheries quickly became highly efficient and shark catches increased markedly (Lorrance and DuPuoy, 1998; Pineiro *et al.*, 1998), and at present new high-technology fishing vessels are being built to exploit deepwater sharks (Anon., 2000a). Concerns about directed shark fisheries are based on a history of stock collapses and rapidly declining catch rates, in addition to the constraints of elasmobranch life history strategies (Holden, 1977). Nevertheless deepwater fisheries are growing rapidly (Hopper, 1995) at a faster rate than the collection of adequate scientific information for their management (Merrett and Haedrich, 1997). Reflecting on the by-catch of sharks in deepwater fisheries off New Zealand, Bonfil (1994) recommended that since the effect of fishing on these sharks was unknown, more research into the biology, population structure and the levels of

discarding would be required. This statement applies equally to the situation west and north of Ireland. It is the purpose of this study to further the knowledge of the biology, population structure and discarding of such deepwater shark species.

1.1 Exploitation of deepwater sharks

While there are several fisheries for deepwater sharks in the northeast Atlantic, the trawl fishery that developed in the Rockall Trough, and on the slopes of the Porcupine Bank is one of the most intensive. Exploratory trawling of these areas in the 1970s found that sharks were dominant species in the catch (Bridger, 1978). This author considered that the viability of deepwater fishing in these areas would depend on finding markets for the sharks. Although there was a French fishery for blue ling *Molva dypterygia* in the 1970s targeting of other deepwater species only began in 1989 when some larger French trawlers (Plates 1.1 and 1.2) diversified onto the continental slope as shelf stocks became less lucrative (Charuau *et al.*, 1995). Two species of sharks are routinely landed for their flesh and livers *Centrophorus squamosus* and *Centroscymnus coelolepis*, collectively called "siki" (Gordon, 1999). Landings of sharks increased from 302 tonnes in 1991 to 3,284 tonnes in 1996 (Anon., 2000b). Since the mid 1990s a new fleet of Scottish trawlers has begun to target deepwater species, including sharks. Furthermore, a new deepwater trawl fishery has developed on the Hatton Bank, northwest of Ireland and is prosecuted by a fleet of large Spanish trawlers. Total landings of deepwater sharks from this fleet were 554 tonnes in 1997, mainly *Centroscymnus coelolepis* (Gordon, 1999). Official landings data of all deepwater species including sharks are presented in Table 1.1 and official shark landings data by country are presented in Table 1.2. Apart from France no other country reports landings data for deepwater sharks, but rather for shelf and slope species combined.

A long-line fishery for deepwater sharks began in 1991 in the waters west and north of Ireland and Britain. Before that time deepwater fishing was technologically too difficult and the fish unmarketable. But as the target species of many Spanish long-liners, hake *Merluccius merluccius* ceased to be profitable, boats began to fish for deepwater sharks (Iglesias and Paz, 1995). These vessels also fish the continental slopes of the Bay of Biscay and the north west coast of Spain (Pineiro *et al.*, 1998). While some of the catches from these vessels are landed into Spanish ports, those quantities never exceeded

350 tonnes per annum (Pineiro *et al.*, 1998). However it seems likely that much of the official shark landings of English and Welsh vessels (Table 1.2) consist of deepwater species as most Spanish long-line vessels are registered in those countries (Iglesias and Paz, 1995). Evidence for this assumption can be found in official statistics. In the years 1988 to 1990 annual landings of sharks by English and Welsh boats never reached 40 tonnes. In 1991 there was a marked increase in landings to 201 tonnes. By 1997 annual shark landings were 2,721 tonnes, but declined to 1,812 tonnes in 1998 (Anon., 2000b). Before 1991 landings of sharks probably consisted of shelf dogfish and other sharks. The new fishery for deepwater sharks inflated the landings figures from 1991 onwards.

A small long-line fishery for deepwater sharks also developed on the north and northwest coasts of Spain with vessels targeting sharks, mora *Mora mora* and forkbeard *Phycis blennoides* (Iglesias and Paz, 1995). The main shark species in this fishery are *Centrophorus squamosus, Centroscymnus coelolepis, Deania calceus,* kitefin shark *Dalatias licha,* blackmouth dogfish *Galeus melastomus,* and lesser spotted dogfish *Scyliorhinus caniculus* and rose from 31 tonnes in 1991 to 711 tonnes in 1996 (Pineiro *et al.*, 1998). Further south several small long-line fisheries exist on the Portuguese coast (EC FAIR, 1999). In the late 1980s the main species in landings was *Centrophorus granulosus*, but landings of this species have declined ever since. Figures for 1998 show 428 tonnes of *Centrophorus squamosus* with 544 tonnes of *Centroscymnus coelolepis*. There was a marked decline in landings of gulper shark *Centrophorus granulosus* from 1,056 t in 1989 to 147 tonnes in 1998 (Anon., 2000b). There is a directed long-line fishery for *Dalatias licha* at the Azores and in the early 1980s this species accounted for about one fifth of total Azorean fish landings (Silva, 1983). Landings from this fishery have declined from 896 tonnes in 1991 to 31 tonnes in 1999. In the most recent years small numbers of *Centrophorus squamosus* have also been landed in this area. A small long-line fishery for *Centrophorus squamosus* and *Centroscymnus coelolepis* also exists at Madeira but landings never exceeded 30 tonnes throughout the 1990s (Anon., 2000b).

Deepwater shark fisheries elsewhere in the world are less well documented. Yano and Tanaka (1984) state that sharks of the genera *Centrophorus, Centroscymnus* and *Deania* have been exploited in Suruga Bay, Japan, since the 1940s for liver oil. This oil is used for lubricants, extracts of vitamin A and the squalene content is used for cosmetics and health foods. The demand for liver oil as a lubricant was greatest during World War II

(Nakano, 1999). Indeed Suruga Bay and Sagami Bay were famous fishing grounds for deepwater sharks (Tarumoto, 1984, cited in Nakano, 1999). Japanese demand for shark livers led to the development of a deepwater shark fishery off Sri Lanka in the 1940s. However this fishery had almost ceased by 1980, though a small revival took place in more recent years (Joseph, 1999). Compagno (1984) notes that *Centrophorus granulosus, C. lusitanicus* and *C. niaukang* are exploited for their livers in fisheries off Taiwan. Some information on this fishery is presented by Yang (1979). Anderson and Waheed (1999) state that *Centrophorus niaukang, C. tessellatus* and *C. squamosus* are "major target species" in the Maldives. In New Zealand waters about 4 % of elasmobranchs landed consisted of deepwater sharks and rays (Bonfil, 1994). *Dalatias licha* appears to be the most important species with landings of between 100 and 400 tonnes per annum for 10 years until 1997. About 200 tonnes of *Deania calceus* per annum were landed in the 1980s but by 1997 landings had declined to 21 tonnes (Francis and Shallard, 1999). In Australian waters *Centroscymnus owstoni, C. coelolepis* and *C. crepidater* along with *Deania calceus* are a by-catch in fisheries for orange roughy *Hoplostethus atlanticus*. Recently squalid sharks have supported liver oil fisheries off the south Australia (Gordon, 1999 and references therein).

The main fisheries for deepwater sharks are summarised above. However the difficulty in obtaining accurate landings data for individual species (Anon., 2000b) means that accurate figures are available for only the smaller fisheries, off Iberia and the oceanic islands of the Atlantic. In some fisheries a marked downward trend in landings of target species is evident; *D. licha* at the Azores, *C. granulosus* off Portugal (Anon, 2000b). Though such declines may be due to market considerations rather than stock depletion (Francis, 1998; Gordon, 1999).

Table 1.1. Official landings (tonnes) of deepwater species in ICES Sub-Areas* VI and VII, corresponding to area of study. Data for sharks are not exclusively for deepwater species. Moridae are not segregated from *Phycis blennoides*.

Species	1988	1989	1990	1991	1992	1993	1994	1995	1996	1997	1998	1999
Beryx spp.	0	12	8	0	3	1	5	3	178	25	81	78
Argentina silus	10,439	25,559	7,294	5,197	5,906	1,577	5,707	7,546	5,863	7,301	5,555	265
Molva dypterygia	9,288	9,422	5,964	6,235	6,645	5,526	4,355	4,839	6,915	6,866	7,278	8,169
Aphanopus carbo	0	154	1,060	2,759	3,436	3,529	3,101	3,278	3,689	2,995	1,967	1,631
Phycis blennoides	1,898	1,815	1,921	1,574	1,640	1,462	1,571	2,138	3,590	2,335	3,040	2,176
Molva molva	28,092	20,545	15,766	14,684	12,671	13,763	17,439	20,856	20,838	16,668	19,863	14,811
Moridae	0	0	0	1	25	0	0	0				
Hoplostethis atlanticus	0	8	17	4,908	4,523	2,097	1,901	1,039	995	1,039	1,071	1,401
Chimaeridae	0	0	0	0	0	0	2	0			0	
Coryphaenoides rupestris	32	2,440	5,730	7,793	8,338	10,121	7,860	7,767	7,095	7,070	6,364	5,747
Pagellus bogaraveo	252	189	134	123	40	22	10	36	33	36	13	15
Sharks	85	40	345	1,438	3,441	4,818	5,473	6,224	5,460	6,224	5,590	3,743
Aplepocephalidae	0							7		7		
Brosme brosme	3,002	4,086	3,216	2,719	2,817	2,378	3,233	1,832	2,417	1,832	1,775	1,775
Polyprion americanus	7	0	2	10	15	0	0	0	83	0		

* ICES fishing areas are shown in Fig. 1.12.

Table 1.2. Official landings (tonnes) of sharks in ICES Sub-Areas VI and VII by country. Only France provides data for deepwater species (*Centrophorus squamosus* and *Centroscymnus coelolepis*). Data for other countries include non deepwater species.

	Faroes	France*	Germany	Spain	Norway	England/ Wales	Scotland	Total
1988						19	0	19
1989						32	8	40
1990		302				38	5	345
1991		1,184				201	53	1,438
1992	3	2,802				503	133	3,441
1993		3,426	124			821	447	4,818
1994		3,609	395			742	727	5,473
1995		3,417	2			1,315	782	5,516
1996		3,284	276			1,345	555	5,460
1997		2,984	66	152		2,721	301	6,224
1998		2,567	65	645		1,812	501	5,590
1999		1,839	189	199	13	1,403		3,743

1.2 The deepwater environment of the continental slopes

The deep sea is the largest habitat on earth (Merrett and Haedrich, 1997). Marshall (1979) defined the deep sea as all regions below the permanent thermocline. The European Communities considers it to comprise all waters below 500 m, while the International Council for the Exploration of the Sea defines the deep sea as all waters deeper than 400 m – 500 m. The deep sea habitat can be subdivided into the continental slope 200 m – 2,500 m, continental rise 2,250 m – 4,500 m and the abyssal plain, greater than 4,500 m (Marshall, 1979). The continental slope corresponds to the region of greatest bio-diversity in the temperate ocean (Gordon *et. al.*, 1995a).

Although the continental slopes only account for 8.8 % of the ocean bottom they occupy an important position between the continental blocks and the deep sea floor (Merrett and Haedrich, 1997). The gradient of the continental slopes varies between cliffs to gentle slopes of 1:40 in contrast to the continental shelf and deep sea floor where gradients of less than 1:1,000 are the norm (Gordon *et. al.*, 1995a). The slopes are also characterised by canyons and cliffs (Merrett and Haedrich, 1997). These slopes occupy the boundary layer between the oceanic and continental tectonic plates and are often subject to seismic activity. In the Atlantic, however, the slopes are characteristically devoid of seismic action (Gage & Tyler, 1991). The only other parts of the oceans with such topographical diversity are the mid-ocean ridges. In both cases a great diversity of pelagic and demersal fish species is to be found (Merrett and Haedrich, 1997). Where the gradients are favourable to settlement, sedimentation occurs and the substratum is covered with muds of terriginous and hemipelagic origin (Marshall 1979; Murray and Hjort 1912). A schematic representation of the continental slopes is presented in Fig. 1.1.

Light is rapidly attenuated with depth in the ocean. At depths of 150 m only 1 % of incident light remains. Red is removed first with blue and green penetrating to the greatest depths (Merrett and Haedrich, 1997). Fig. 1.2 shows typical temperature profiles in the deep ocean. The water beneath the thermocline is not homogeneous in temperature or salinity (Gage and Tyler, 1991), nor is it stationary either. Cold bottom water (2,000 m) has been shown to be driven up and down the slope by semi-diurnal tidal variations (Rice *et al.*, 1991). This movement is linked with long-term fluctuations due to spring-neap oscillations (Dickson *et al.*, 1982).

Zonation of seawater masses is a result of density, salinity and temperature (Fig. 1.3) and density is affected by temperature and salinity to differing extents at different latitudes. These variations mean that water masses maintain their integrity over considerable distances as they move with currents from one region to another (Merrett and Haedrich, 1997). There are other forms of water movement in the deep sea too. In the northeast Atlantic, eddies emanating from the Gulf Stream cause benthic storms, analogous to, but more persistent than, atmospheric anti-cyclones. Other catastrophic events include sediment slides and turbidity currents (Gage and Tyler, 1991). These authors describe a zone, up to 100 m thick, above the sea floor, where friction of water causes mixing. This is termed the Benthic Boundary Layer, the thickness of which is determined by the velocity of the currents involved.

Photosynthetic activity occurs only in the upper 200 m of the ocean, and this surface layer must support virtually all life beneath it (Merrett and Haedrich, 1997). After the spring plankton bloom detritus sinks rapidly to the sea floor at a rate of more than 100 m per day (Rice *et al.*, 1986). The seasonality of this input is thought to be a cause for seasonal cycles of reproduction in some deepwater organisms (Tyler, 1988). Thus, the sea floor acts as the ultimate sink of all primary production (Gordon *et al.*, 1995a). Biomasses of the benthos and of demersal fishes are broadly similar. If the benthos supplies all the trophic requirements of the demersal fish the turnover rates must be high. However there is no evidence that this is so (Gage and Tyler, 1991 and references therein). Therefore demersal fish must obtain some of their nutrient supply from outside sources. One such source is the lateral impingement of mesopelagic organisms on to the slopes. Mauchline and Gordon (1991) describe this phenomenon, whereby the mesopelagic zone comes into contact with the rising slopes and provides prey to demersal fishes there. Another prey source is that provided by epipelagic species whose diurnal vertical migrations bring them into contact with the slopes in part of their range (Mauchline and Gordon, 1991). Slope-dwelling fish feed on organisms in the scattering layers. These organisms move towards the surface at night to feed and retreat to greater depths during the day (Gordon *et al.*, 1995a).

Early students of the deep sea environment considered it to be a refuge for archaic species unable to exist in more competitive environments. However a review of recent

work shows that deepwater fish are often highly adapted for their environment (Merrett and Haedrich, 1997). There is a considerable variation in the vertical ranges of slope dwelling species (Gordon *et al.*, 1995a). Heincke's law, the so-called "bigger-deeper" phenomenon was described for the deepwater eel *Synaphobranchus kaupi* which has a broad depth range from 500 to 2,000 m (Gordon and Bergstad, 1992). However this was found to be an artefact of sampling, whereby larger specimens avoided small trawls on upper and middle slopes of the Porcupine Seabight. In contrast to *Synaphobranchus kaupi* the deepwater sharks have relatively narrow depth ranges (Gordon *et al.*, 1995a). Depth-specific zonation of deepwater fish over wide geographical areas is a recurrent theme in reviews of deepwater biology (Gordon *et al.*, 1995a). However Haedrich and Merrett (1988) found little evidence that demersal fish present in any one area were strongly associated with any other species in a manner that could be described as a community. Furthermore vertical distributions of deepwater species in the water column are poorly understood because mid-water trawls have rarely been used for sampling purposes in the deep sea (Merrett, 1986). Demersal fishes are usually found in discrete vertical ranges. The absence of juvenile stages of deepwater sharks and black scabbard *Aphanopus carbo* in the northeast Atlantic may be due to their occurrence in mid-waters, unavailable to conventional sampling trawls (Gordon *et al.*, 1995a).

Growth of deepwater fish decreases exponentially with increasing age, leading to an accumulation of older age groups and producing characteristic bi-modal length frequency distributions (Gordon *et al.*, 1995a). Validation of age has been accomplished rarely for deepwater fish. The sablefish *Anoplopoma fimbria* was the subject of a validation study by McFarlane and Beamish (1995) who injected these juveniles with tetracycline. Specimens attained ages of 70 years. Gordon *et al.* (1995b) validated ages of juvenile roundnose grenadier *Coryphaenoides rupestris* by edge analysis of otolith sections. The otolith section method showed that this species attained ages of 60 years (Kelly *et al.*, 1997a). Reproduction in deepwater fish may not be an annual phenomenon (Gordon and Mauchline, 1996). Analysis of a spawning aggregations of orange roughy *Hoplostethus atlanticus* found that only 42 % were in reproductive state (Bell *et al.*, 1992). These authors suggested that limited resources led to intermittent spawning. Unlike many shelf-dwelling teleosts, deepwater species only mature when somatic growth has almost ceased (Gordon *et al.*, 1995a). Many deepwater species only mature at large size and

age; the orange roughy *Hoplostethus atlanticus* at 20 – 25 years (Clark, 1995) and the roundnose grenadier *Coryphaenoides rupestris* at 7 – 11 years (Kelly *et al.*, 1997a).

Slope-dwelling fish form mixed communities with many species equally vulnerable to fishing. The less dominance there is in a fish community, the greater the by-catch and discarding is likely to be (Merrett and Haedrich, 1997). Connolly and Kelly (1996) estimated that trawling in the Rockall Trough alone might result in the discarding of 26.5 million individuals, annually, of at least 30 species. Because so many species on the slope have over-lapping depth ranges and because fishermen will target certain depths to maximise catch rates of target species, fishing is likely to impact on the entire fish community (Gordon *et al.*, 1995a). A considerable knowledge base is required in order to determine which (if any) deepwater species could sustain commercial fisheries (Hopper, 1995; Merrett and Haedrich, 1997).

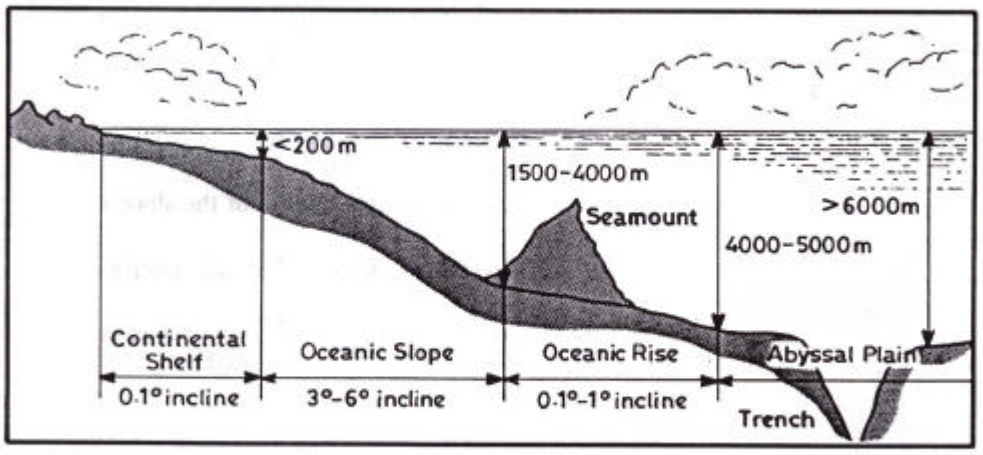


Fig 1.1. Continental. shelf, slope and rise, redrawn from Hopper (1995).

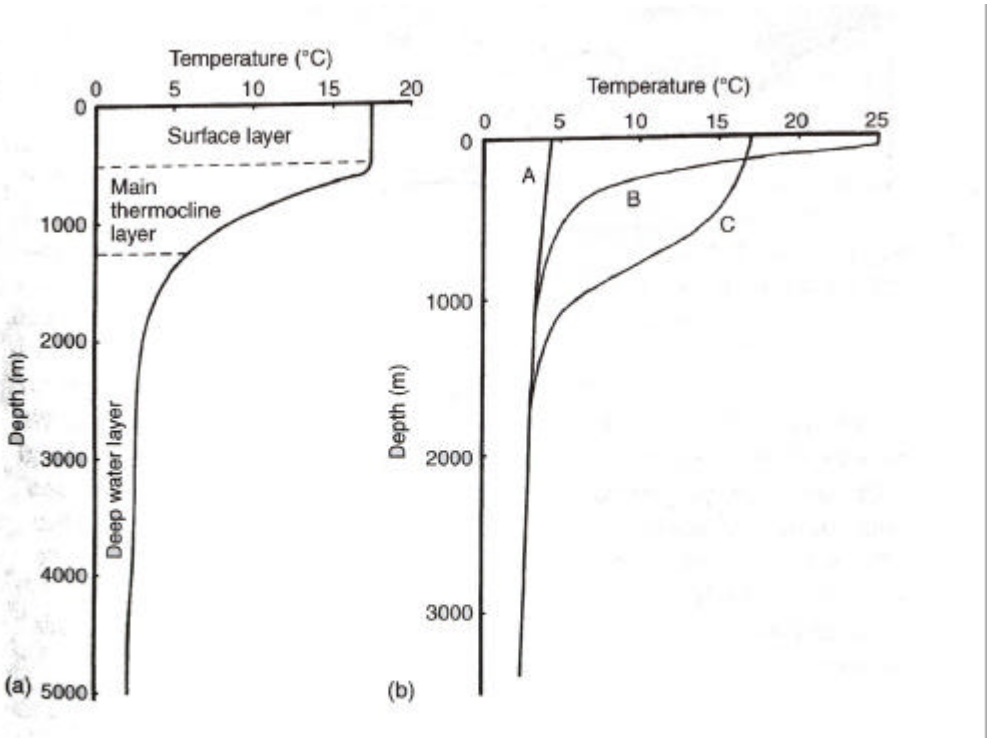


Fig. 1.2. Schematic temperature variation with depth in the deep ocean (a). Typical temperature profiles in winter (b); A, high latitudes, B, near the equator and C, middle latitudes. After Charnock (1971) and redrawn from Merrett and Haedrich (1997).

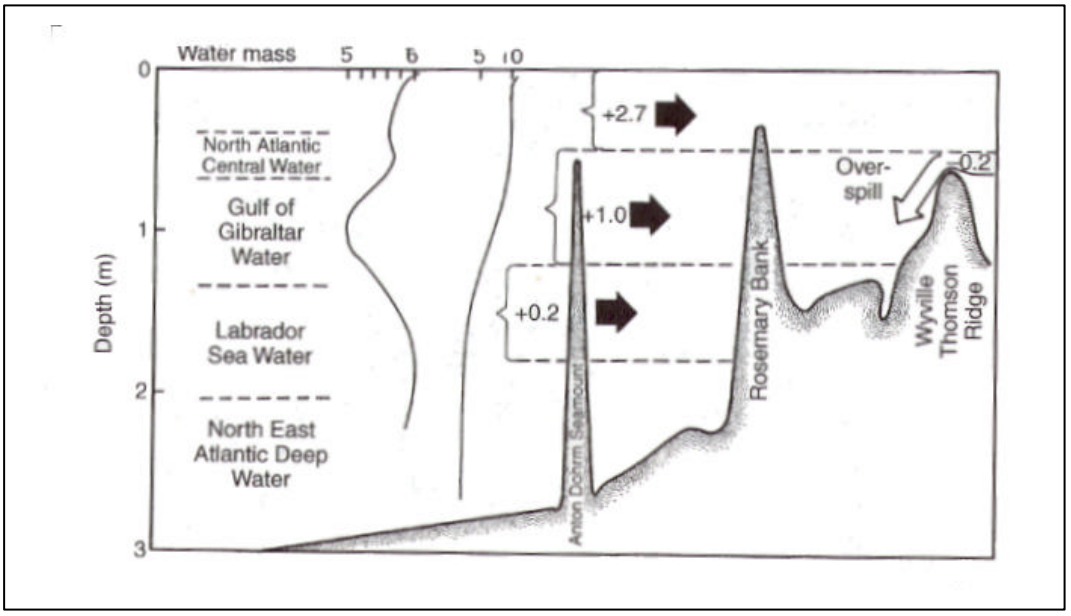


Fig. 1.3. Oxygen and water mass circulation profile patterns in the Rockall Trough, redrawn from Mauchline (1986).

1.3 The Study Area

The area under study comprises the continental slopes west and northwest of Ireland between 49^0 N and 59^0 N (Fig. 1.4). This area of the continental slope can be divided into four separate regions: the Hebrides Terrace, the Donegal Terrace, the Porcupine Slope and further south, the Porcupine Seabight. Between the first three areas and the Rockall Bank lies a deep basin – the Rockall Trough. To the south of the Porcupine Bank lies the Porcupine Seabight (Ellett *et al.*, 1986). Both the Rockall Trough and the Porcupine Seabight deepen progressively to join the Porcupine Abyssal Plain at around 4,000 m on the deep ocean floor (Mauchline *et al.*, 1986). Extensive areas of productive deep water such as this only exist in a small number of areas of the northeast Atlantic; the Reykjanes Ridge, northeast Canada and Faroe-Shetland Channel. However the Rockall Trough is probably the best-documented slope area of any ocean (Mauchline, 1990). Within the area of reference most scientific study has concentrated on the Rockall Trough and the Porcupine Seabight, other areas being poorly described.

1.3.1 Geology

Sea bed sediments are derived from 3 sources: 1) terrigenous muds carried out over the continental shelf; 2) faecal and detrital fallout; 3) sedimentation of matter trapped from the atmosphere by surface tension (Murray and Hjort 1912). The terrigenous sediments are coarse in nature and found on the continental slope and rise where they are transported by turbidity currents and sediment slumps. These deposits are richly organic which may explain the relatively high productivity of the associated benthos (Rice *et al.*, 1991). The rate of deposition of sediments derived from fallout is dependent on the productivity of the overlying water. On the western European shelf margin this sedimentation is seasonal and forms an ooze, rich in calcite (in depths above the calcium compensation point) and silica. The sediments of airborne origin are thickest in ancient areas and passive margins, such as the Porcupine Abyssal Plain. Accumulation of this type of sediment is very slow (Gage and Tyler, 1991). The absence of canyons on the western slopes of the Porcupine Bank and of the Porcupine Sea Bight are thought to reflect a limited sediment supply (Rice *et al.*, 1991).

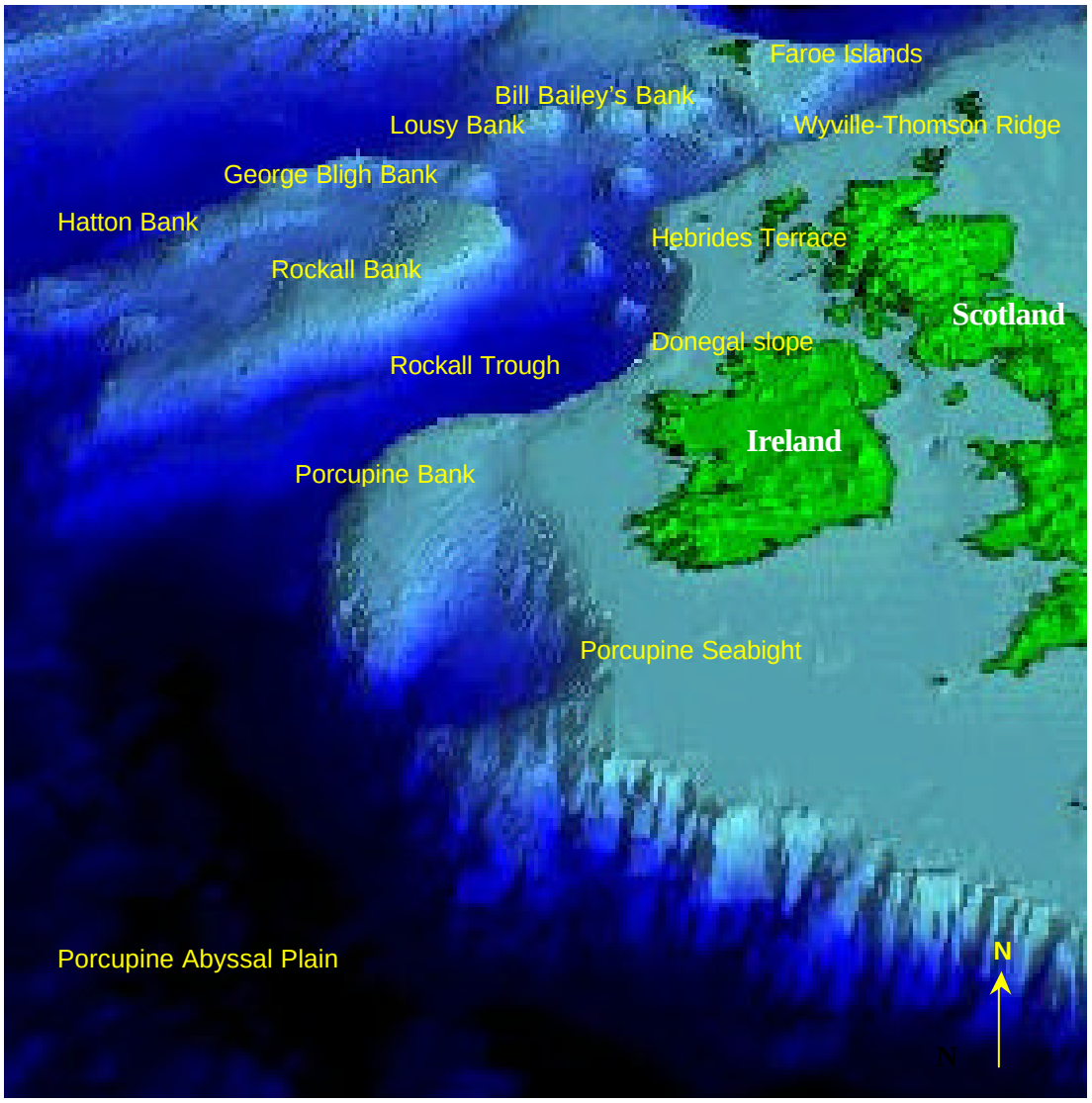


Fig. 1.4. Bathymetric map of the study area showing main topographical features.

1.3.2 Hydrography

The hydrography of the region is the subject of several reviews (Ellett *et al.*, 1986; Mauchline, 1990 and Rice *et al.* 1991). Oxygen and salinity profiles characterise the water masses of the Rockall Trough. Temperature drops from 9.5^0C in the upper layers (250 m) to about 5.5^0C at 1,250 m depth (Ellett *et al.*, 1986). North Atlantic central water is present at around 750 m, and is underlain by Gulf of Gibraltar water (high temperature and salinity but low oxygen) to 1,500 m. Below this is Labrador Sea water to 2,000 m, underlain by Norwegian Sea water overspilling from the Wyville-Thomson Ridge. Neither of the intermediate zones is detectable by temperature (Mauchline, 1990). Northeast Atlantic (> 2,000 m) water is not present in the Rockall Trough as it becomes shallower towards the northeast end. This shallowing may cause mixing (Mauchline 1990). These hydrographic characteristics of the Rockall Trough are illustrated in Fig. 1.3.

In the Porcupine Sea Bight eastern North Atlantic water is detectable to depths of 750 m. Beneath this is Mediterranean water, with a maximum salinity and minimum oxygen at depths of 950 m. Below the Mediterranean water is Labrador Sea water with a salinity minimum and oxygen maximum at about 1,700 m. A small increase in salinity at 1,900 m indicates the influence of Norwegian Sea water from north of the Wyville-Thomson Ridge (Rice *et al.*, 1991). A nett north eastward flow of water has been described in the Rockall Trough between 500 and 1,200 m and is associated with a southward flowing current on the western slopes. Cold, dense water from 2,000 m flows in currents enhanced by semi-diurnal tidal variations up and down the slope (Rice *et al.*, 1991). Another type of water movement in this area is the eddie. Eddies develop as spin-offs from the Gulf Stream. High wind and stormy seas may also form such movements. These movements are analogous to anticyclones in the atmosphere, though they tend to endure for longer periods of time. They distribute kinetic energy downwards (Gage and Tyler, 1991). Hydrographic mechanisms occur which will retain populations of a species in the Rockall Trough for periods of 3-6 months (Mauchline, 1986). No clear evidence exists that the northward flowing boundary current in the eastern North Atlantic enters the Porcupine Sea Bight (Dickson *et al.*, 1982)

1.3.2 Biology

Several accounts exist of the biology of the Rockall Trough; Gage and Tyler (1991), Gordon and Duncan (1985), Gordon *et al.* (1995a), Mauchline (1986) and Mauchline (1990). In addition, a bibliography for the area has been produced by Mauchline *et al.* (1986). Gordon *et al.* (1995a) describe the differing temperature regimes either side of the Wyville-Thompson Ridge. At depths down to that of the ridge, temperature profiles are similar on both sides. However, the rate of decrease in temperature with depth east of the ridge is much more rapid than the decrease to the west. The different temperature profiles either side have an effect on the icthyo-fauna. Peaks of species diversity and biomass are between 1,000 m and 1,500 m in the Rockall Trough, while in the Norwegian Basin biomass and diversity decrease below 500 m. This is clearly evident either side of the Wyville-Thompson ridge. To the north temperature and salinity rapidly decrease to 4^{0}C and 35 ‰ respectively, while to the south these parameters are found at 1,600 m. The Boreal fauna north of the ridge is mirrored by a similar assemblage of species at depth in the Rockall Trough (Gordon *et al.*, 1995a). Expatriate species are supplied to the Norwegian Sea via the Wyville-Thomson Ridge from the Rockall Trough (Mauchline, 1986).

Direct measurements of primary productivity are not available for the Porcupine Seabight (Rice *et al.*, 1991). However a strong correlation exists between surface productivity and the arrival of sedimentary material at depth. Indeed this phenomenon was first described from the this area (Rice *et al.*, 1986). This seasonal arrival of phytodetritus is assumed to be a cause for seasonal reproduction cycles of some deepwater organisms (Tyler, 1988).

Demersal fish catches on the upper and middle slopes of the Rockall Trough are dominated by Alepocephalidae and black scabbards *Aphanopus carbo*, along with Squalidae, in commercial trawls, but were poorly represented in other types of nets (Gordon and Duncan, 1985). In the Porcupine Seabight the dominant group in terms of species richness was the Macrouridae, followed by the Squalidae, Gadidae and Alepocephalidae (Merrett *et al.*, 1991). These authors tentatively concluded that biomass and abundance were lower in the Porcupine Seabight than other deep water areas west of Ireland. This finding accords with that of Bridger (1978) who recorded lower catch rates

of demersal fish in this area. Non-commercial gears may underestimate the overall biomass of the region (Gordon and Duncan, 1985). Diurnal migrations are thought to cause difficulties in obtaining representative samples for all age groups of particular organisms (Mauchline, 1986).

While this area is probably the best studied deepwater area in the world, surprisingly few studies exist of deepwater squalid sharks, despite their dominance. The first detailed account of the shark fauna was that of Bridger (1978) who described the catch rates and abundances of the main species. Mauchline and Gordon (1983) described the diets and trophic relationships of the squalid species of the Rockall Trough, while trends in abundance and biomass by depth range have been dealt with by Gordon and Swan (1997) and Gordon (1999). A recent paper describes the main aspects of the reproductive biology of two species present, *Centrophorus squamosus* and *Centroscymnus coelolepis* (Girard and Du Buit, 1999).

1.4 Previous studies

Relatively few studies on deepwater sharks exist in the scientific literature. However the majority deal with members of the Squalidae, reflecting, perhaps, their commercial importance. The approach taken here is to describe the knowledge base of the three species of squalid sharks under study, in the light of the broader elasmobranch literature. The emphasis has been placed on other Squaliform sharks, particularly the deepwater species. However other groups are dealt with in certain instances, where it was considered relevant to do so. Accounts in the literature of the biology and fisheries of each species under study are presented in Table 1.3.

1.4.1 General biology and population structure

The Squalidae, or dogfish, include a great variety of species of small to giant sharks, and have attained greatest diversity in deep water (Compagno, 1984). Indeed the Squalidae are one of the most widespread and abundant families of sharks. They have a vast geographic and bathymetric range, occurring in all seas from Arctic to sub-Antarctic in coastal waters down to depths of over 6,000 m (Compagno, 1984). However the systematics of these fish are currently in a state of flux with recent works dividing them into several families (Compagno, 1999a and b). In particular the genus *Centrophorus* has been the subject of several reviews (Guallart-Furio, 1998; Muñoz-Chapuli and Ramos, 1989) and is considered to require an urgent revision (Gordon, 1999).

The majority of studies on the squalid sharks have concentrated on the spurdog *Squalus acanthias*, reflecting its importance in commercial fisheries. It is regarded as the best-known species of shark (Compagno, 1984). The remaining species of the family are much less well understood. Population structure of *Squalus acanthias* has been the subject of much study. It is known to undertake extensive movements including trans-Atlantic migrations (Templeman, 1976), but tagging studies around Ireland and Britain led Vince (1991) to conclude that the spurdogs present in the NE Atlantic belong to one large stock. This species is also known to make movements according to the reproductive cycle. Off New Zealand, parturition, mating and ovulation took place in deep off-shore waters according to Hanchet (1988), though mid-term gestating females moved inshore for a while. These findings conflict with those of Templeman (1944) who

suggested that parturition takes place in shallower waters. Ketchen (1986) demonstrated that parturition actually took place in mid-waters, a finding which Hanchet (1988) considered as an explanation for the relative absence of post-natal females from the sea-bed during the breeding season.

Segregation within squalid shark populations has been described by several authors. In particular there is a well-documented tendency for depth segregation in reproductive behaviour. Pregnant and ovulating females occurred in the shallowest portion of the bathymetric range of *Centroscymnus owstoni* in Suruga Bay, Japan, while immature specimens were found in deeper waters (Yano and Tanaka, 1988). These authors did not find any evidence of segregation among males. Near New Zealand, however, Wetherbee (1996) noted segregation by size and sex for populations of *Etmopterus granulosus*. Such segregations may not be confined to squalids, since the frilled shark *Chlamydoselachus anguineus* also displayed a segregation by reproductive stage (Tanaka *et al.*, 1990). Muñoz-Chapuli (1984) put forward a hypotheses for demersal sharks in respect of segregation by size and sex. Based on bathymetric distributions of a number of species, including *Centrophorus granulosus* and *Galeus melastomus*, he hypothesised that that adults mate at depth and the young are born in shallow water nursery areas towards the top of the continental slope. Data on *Deania calceus* from New Zealand might support this theory. Newly born sharks were found in shallow depths along with large females while the proportion of males increased with depth (Clark and King, 1989).

Segregation between species has been a subject dealt with by several authors. In a study of Suruga Bay, Japan, *Centrophorus acus* was shown to swim parallel to the 500 m contour line, and, though this species did move into shallow waters occasionally, it was found to stay within a relatively narrow depth range. The three species of this genus present displayed a marked degree segregation by depth (Yano and Tanaka, 1986). *C. coelolepis* was found to occur deeper than *C. owstoni* in the same area (Yano and Tanaka 1983a). Three species of the genus *Centrophorus* displayed marked bathymetric segregation in Suruga Bay, Japan (Yano and Tanaka, 1983a). Depth segregation within genera was also described from southwest Africa, where *Deania creipdalbus* occurred in shallower waters than *D. calceus* (Yano, 1991). Perhaps this segregation is due to trophic considerations as suggested by Ebert *et al.* (1992) who described the differing prey preferences by *Squalus* and *Etmopterus* species off southwest Africa. The absence

of *Centroscymnus coelolepis* from the upper slopes of the western Mediterranean was attributed to the occurrence of *Etmopterus spinax* at these depths and to differing diets (Carrasson *et al.*, 1992). Differing depth ranges allows deepwater squalid sharks to avoid competition for food resources in the Rockall Trough, according to Mauchline and Gordon (1985). Multivariate analysis of species composition in this area found that depth accounted for most of the variance within trawl catches (Gordon and Bergstad, 1992). Gordon (1999) clearly demonstrates how biomass, abundance and species composition vary with depth in this area.

The dietary preferences of deepwater sharks were the subject of a study in the Rockall Trough (Mauchline and Gordon, 1983). These authors classified sharks into two groups viz. micro-nekton feeders (*Etmopterus spinax, E. princeps, Centroscymnus crepidater, Apristurus* spp.) and demersal fish feeders (*Centroscyllium fabricii, Deania calceus, Centrophorus squamosus, Centroscymnus coelolepis*). Maximum biomass of sharks was recorded in the depth range 750 m – 1,250 m, corresponding to maximum lateral impingement of meso- and bathy-pelagic fauna. The micro-nekton feeders tended to occur at well above the seabed, while the demersal fish feeders appeared to cruise over the bottom (Mauchline and Gordon, 1983).

A recurrent feature of many studies of deepwater squalid sharks is that small length-groups are often missing. This has been described from Suruga Bay, Japan (Yano and Tanaka, 1983a), the Mid-Atlantic Ridge (Hareide and Thomsen, 1997), at the Azores (Silva, 1988), west of British Isles (Girard and Du Buit, 1999) and southwest Africa (Ebert *et al.*, 1992; Yano, 1991). However this is not a feature of all studies of the group because several authors have documented complete or almost complete length ranges. Such studies include that of Yano and Tanaka (1983a) on *Centrophorus* and *Deania* species, Ebert *et al.* (1992) for *Centrophorus* and *Centroscymnus* species, Clark and King (1989) for *Deania calceus* and Yano and Kugai (1993) for *Centrophorus niaukang*. The reasons for reported presence or absence of small specimens in these studies have not been adequately explained to date. Since most of theses studies were based on bottom trawl sampling, it is possible that smaller size ranges were missed because they occur higher in the water column. Clark and King (1989) used mid-water trawls but unfortunately did not state from which gears they recorded small *Deania calceus*. Gordon *et al.* (1995a) already suggested that small specimens might occur in more

pelagic waters. But it is still not possible to verify this theory or that of Muñoz-Chapuli (1984) that they occur on the shelf edge.

The squalid sharks have relatively large livers, accounting for about 22 % of body weight of *Centroscymnus owstoni* (Higashi *et al.*, 1953) and these livers have formed the basis of important fisheries, such as that in Suruga Bay, Japan (Yano and Tanaka, 1984). An important role of the elasmobranch liver first became apparent in the Irish fishery for basking shark *Cetorhinus maximus*, when this organ was removed it was discovered that the carcass sank rapidly (Morris, 1836, in Went and Ó Súileabháin, 1967). Later Hickling (1930) noted that since the liver of *Squalus acanthias* was rich in oil, it must act as an organ of flotation. Squalid livers have been shown to contain low density hydrocarbons, including squalene (Corner *et al.*, 1969) and it is this substance which appears to allow these species to maintain near-neutral buoyancy (Bakes and Nichols, 1995; Corner *et al.*, 1969). A study of six coastal sharks found that only *Squalus acanthias* had significant quantities of low-density lipids, while the other species had negligible amounts (Craik, 1978b). Craik suggested that the other species, all benthic in habit, did not require low-density lipids, while deepwater and pelagic species needed them for buoyancy. The body morphology of several squalid sharks indicated a slow but sustained, swimming speed, supporting the view that they are neutrally buoyant (Tabit, 1993).

1.4.2 Reproduction

The reproductive anatomy of the male consists of the testes, accessory glands, genital ducts and secondary sex organs (Wourms, 1977). The principal secondary sex organs are the claspers, which are modifications of the pelvic fins (Dodd, 1983). The testes in all elasmobranchs are paired, elongate, dorso-ventrally flattened organs supported by a mesorchium (Hamlett, 1999). In many species the testes are embedded in lymphomyeloid tissue, the epigonal organ as described by Matthews (1950). Epigonal organs were not visible at a macroscopic level in *Centroscymnus coelolepis* or *C. owstoni*. The testis performs the dual functions of producing germ cells and steroid hormones (Hamlett, 1999). A survey of elasmobranch testes has shown three structural types, radial, diametric and compound (Pratt, 1988). Squalid sharks along with charcharhinid and sphyrnid species have testes conforming to the diametric type (Fig.

1.5). Pratt's classification is based on the arrangement of the spermatogenic zones visible in cross-sections of the testes.

The structure of the elasmobranch testis is almost unique in that the basic structural unit is the spheroidal ampulla, not the tubule as in most vertebrates (Dodd, 1983). Grier (1992) proposed that the ampulla be re-defined as the spermatocyst. The spermatocysts proliferate from the meso-ventral area of the testis (Hoar, 1969). Spermatocysts near the efferent ducts contain ripe spermatozoa (Mellinger, 1965). Sections of a diametric testis show the progression of spermatocyst development from the germinal zone to the zone of degenerating spermatocysts where the spermatozoa are released (Parsons and Grier, 1992; Simpson and Wardle, 1967).

The female reproductive system in elasmobranchs consists of paired or single ovaries and oviducts (Hamlett and Koob, 1999). The ovary is suspended by the mesovarium (Wourms, 1977) and the ovary contains stroma, pre-vitellogenic oocytes, in mature females large yolky oocytes and pre- and post-ovulatory follicles (Dodd, 1983). The ovary performs three functions viz. production of germ cells, acquisition and storage of yolk and production of hormones (Hamlett and Koob, 1999). The germinal epithelium from which follicles emerge covers the outer surface (Hoar, 1969). Elasmobranchs typically produce small numbers of large ova (Wourms, 1977). There is little information on oogenesis or oocyte dynamics in elasmobranchs, in contrast to the situation in teleosts which have been well described (Wallace and Selman, 1981 and references therein). Dodd (1972) described the ultrastructure of the ovarian follicle of *Scyliorhinus canicula* while Lukina (1987) conducted a similar study of *Squalus acanthias*. Atretic follicles are present in the ovaries of most elasmobranchs (Dodd, 1983). The amount of yolk present in these structures depends on when they formed during follicle development (Hamlett and Koob, 1999). Following ovulation the follicle collapses and a *corpus luteum*, with invading granulosa forms (Hisaw and Hiasw, 1959). These authors felt that these structures did not have an endocrine role as do *corpora lutea* in mammals. One study of ovulation showed that ova are shed into the peritoneal cavity and directed towards the ostium by cilliary movement (Metten, 1939). The oviducts undergo specialisation in various species according to the reproductive mode (Dodd, 1983). In viviparous species the lower oviduct is developed as a uterus (Budker, 1958).

All recent elasmobranchs employ internal fertilisation (Wourms, 1977) and this implies behavioural, morphological and physiological adaptations (Hamlett and Koob, 1999). Two separate reproductive modes have been considered viz. oviparity and viviparity (Hamlett and Koob, 1999; Wourms, 1977). Within the viviparous category is a diverse array of differing reproductive modes. These include oophagous embryos (Budker, 1958; Hamlett, 1989; Otake, 1990; Yano and Musick, 1992), placental nutrition of embryos (Castro and Wourms, 1993; Hamlett, 1990; Otake and Mizue, 1985) and placental analogues (Hamlett *et al.*, 1985; Wourms, 1981). Of deepwater elasmobranchs, the Mitsukurinidae (Merrett and Haedrich, 1997) and Pseudotriakidae (Yano, 1992) are oophagous vivipares while the Scyliorhinidae and Rajidae are oviparous (Merrett and Haedrich, 1997). All squalid sharks are viviparous (Wourms, 1977) and all squalids described to date are yolk-sac dependent (Compagno, 1984). Older studies tended to refer to yolk-sac dependent species as "ovoviviparous" though Budker (1958) and Hoar (1969) stated that this was an artificial classification between the oviparous and viviparous categories. This reproductive mode is utilised by about one quarter of extant sharks (Hamlett and Koob, 1999). Various authors have described aplacental viviparity in the squalidae; *Centrophorus atromarginatus* (Tanaka *et al.*, 1978), *Centrophorus granulosus* (Capape, 1985), *Centroscymnus* species (Yano and Tanaka, 1987), *Centrophorus niaukang* (Yano and Kugai, 1993), *Centrophorus squamosus* (Girard and Du Buit, 1999), *Squalus mitsukurii* (Otake, 1990) and *Squalus acanthias* (Ford, 1921).

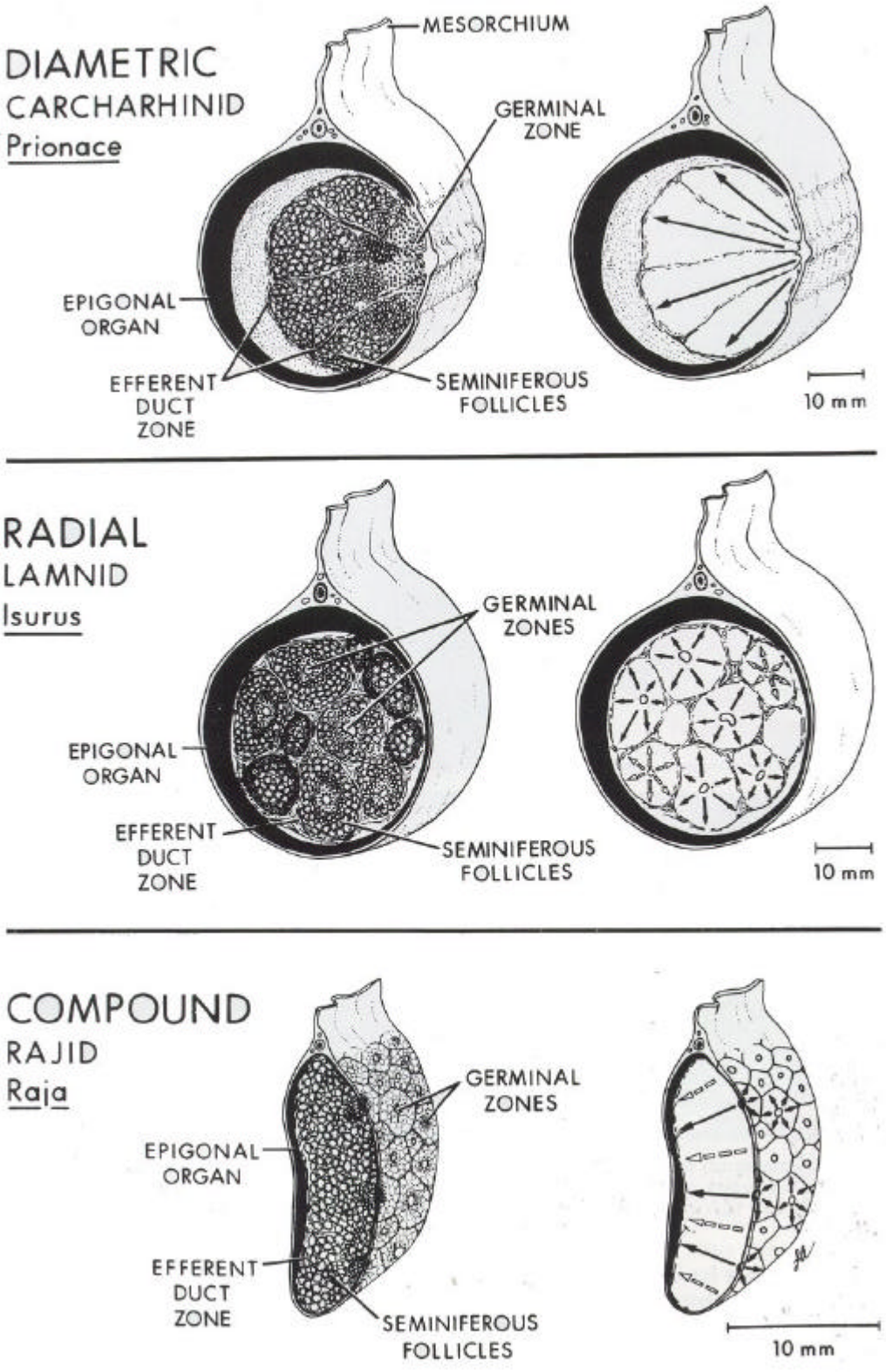


Fig. 1.5. Classification of elasmobranch testis structure (Pratt, 1979).

1.4.2.1 Maturity

Several authors have stated that reproductive strategies are a limiting factor in elasmobranch fisheries (Hoenig and Gruber, 1990; Holden, 1973; Holden, 1974; Pratt and Casey, 1990). In view of the diverse array of reproductive modes employed by elasmobranchs (Hamlett and Koob, 1999; Wourms, 1977) it is not surprising that elasmobranchs vary widely in their relative size and condition at sexual maturity (Pratt and Otake, 1990). These authors recommended that in assessing sexual maturity, workers should consider the presence of fully developed sex products as the most precise indicator. Thus clasper or uterine condition alone is a less reliable indicator than the presence of sperm in the terminal storage areas, ripe oocytes or embryos.

Most recent studies of male maturity have considered the condition of the sperm ducts in addition to that of the claspers; Chen *et al.* (1981) for *Squalus acanthias,* Girard and Du Buit (1999) for *Centrophorus squamosus* and *Centroscymnus coelolepis*, Kirnosova (1989) for *Squalus acanthias,* Wetherbee (1996) for *Etmopterus granulosus*, Yano and Tanaka (1988) for *Centroscymnus owstoni* and *Centroscymnus coelolepis* and Yano (1995) for *Centroscyllium fabricii.* Some authors have reported that clasper length is a good indicator of maturity, based on comparisons with internal features (Ellis and Shackley, 1997; Natanson and Cailliet, 1986; Teshima, 1981). Studies of females have normally made use of classifications with varying numbers of stages. The simplest such scales have classified females as immature, maturing or mature (Chen *et al.*, 1981; Ellis and Shackley, 1997; Gauld, 1979; Jones and Geen, 1977c; Yano, 1993; Yano and Tanaka, 1988). More detailed maturity scales have considered various stages of uterine development and post-natal females (Francis, 1980; Girard and Du Buit, 1999; Hanchet, 1988; Tanaka *et al.*, 1990). Clark and King (1989) used an even more detailed scale including females resting after parturition. However these authors did not state how they classified such females.

Fishery scientists have long been interested in finding a single value to represent age or length at sexual maturity in populations (Trippel and Harvey, 1991). There are many reports of length or age at 50 % maturity in the literature. Many authors present maturity ogives but do not state how they estimated 50 % maturity. Such works include Abdel-Aziz *et al.* (1993), Ellis and Shackley (1997), Gauld (1979), Girard and Du Buit (1999),

Hanchet (1988) and Ketchen (1972). It is possible that these authors constructed ogives using a visual inspection of frequency data, though they may have employed the Probit method as described by Bowering (1983) and Mikhaylyuk (1985). Probit modelling has been used by Kirnosova (1989) for *Squalus acanthias*, while McFarlane and Beamish (1987b) used both visual and Probit analysis to estimate 50 % maturity for this species and achieved a good level of agreement. Silva and Ross (1993) used a Logistic model to describe maturity by length. A different approach was taken by Nammack *et al.* (1985) who used regression analysis of arcsine-transformed maturity data. In a survey of methods for estimating 50 % maturity in fish populations Trippel and Harvey (1991) found that visual interpretation gave best estimates of 50 % maturity only in species exhibiting an abrupt maturation. For species with more gradual transitions to maturity, Probit modelling was found to give the best results. Probit modelling worked well for species with slow or variable growth rates, and consequently appears to be the best method for use in studies of sharks.

1.4.2.2 Fecundity

Estimates of fecundity in elasmobranchs are based on the rate of egg production in oviparous species and the number of embryos in the uteri of viviparous species. In the latter case comparisons are often made between ovarian and uterine fecundity (Dodd, 1983). In oviparous forms annual egg production is taken into account in calculating fecundity (Ellis and Shackley, 1997; Richards *et al.*, 1963; Holden *et al.*, 1971). Holden *et al.* estimated an annual egg production of 50 for certain ray species, based on Clark's (1922) study, while Capape *et al.* (1991) estimated up to 140 per year in *Scyliorhinus canicula*. Fecundity is determined both by the number of young or eggs at each spawning and by the frequency of spawning (Holden, 1973). Some evidence of stress-induced ovulation exists (Dodd and Duggan, 1982) which may effect the accuracy of estimates. In viviparous species determination of fecundity is comparatively easier (Holden, 1974). In most cases annual rates are also lower. Most information exists for *Squalus acanthias*. Reported uterine fecundities vary between 3 and 14 (Kirnosova, 1989 and references therein). The lowest recorded fecundity in this species was 1 (Hanchet, 1988). Fecundity has been shown to increase with parent total length (Ketchen, 1972). Therefore estimates of mean production of offspring depends on the length ranges of females in a population (Jones and Geen, 1977c). Holden (1973)

speculated that increased fishing mortality may lead to density-dependent increases in fecundity. Gauld (1979) calculated that females could accommodate as many as 25 embryos, but suggested that physiological constraints, such as gaseous exchange, would probably limit increased fecundity.

Fecundity in viviparous species are often low, as low as 1 in *Centrophorus granulosus* (Capape, 1985), 2 – 6 in *Carcharhinus isodon* (Castro, 1993) and 1 – 11 in *Squatina californica* (Natanson and Cailliet, 1986). In contrast species with comparatively high fecundities include 82 – 135 for *Prionace glauca* (Gubanov and Grigoryev, 1975; Pratt, 1979), and 82 for *Lamna nasus* (Aasen, 1961). Published fecundity information for deepwater squaliform species is in the middle range; 16 – 28 in *Centroscymnus owstoni* (Yano and Tanaka, 1988) and 5 – 26 in *Centroscyllium fabricii* (Yano, 1995). In some instances no gravid females were recorded so estimates are based on ovarian counts. Wetherbee (1996) reported ovarian fecundity of *Etmopterus granulosus* in New Zealand of 7 – 30.

1.4.2.3 Reproductive Cycles

The earliest study of elasmobranch reproduction was that of Aristotle who documented the mating and egg-laying season in *Scyliorhinus canicula* off Greece (Ford, 1921). While many studies have been carried out, the information available on elasmobranch reproductive cycles is limited to a few species, reflecting the difficulty in obtaining sufficiently large samples, over several years (Wourms, 1977). Some species appear to reproduce throughout the year (Ford, 1921, Metten, 1939). Other species have annual cycles, but display peaks of activity at certain times. This pattern was described for *Raja erinacea* by Richards *et al.* (1963) and Fitz and Daiber (1963). However several species have well-defined annual or biennial cycles of reproduction. Annual cycles in the male have been elucidated by histological analysis of the testes as carried out by Simpson and Wardle (1967) on *Squalus acanthias*, by Teshima (1981) on *Mustelus manazo* and *M. griseus* and by Parsons and Grier (1992) on *Sphyrna tiburo*. Seasonal patterns of gonadosomatic index have also highlighted seasonal cycles in male elasmobranchs, for example in *Scyliorhinus caniculus* (Dobson, 1974 cited in Dodd, 1983), *Sphyrna tiburo* (Parsons and Grier, 1992) and *Dasyatis sabina* (Maruska *et al.*, 1996). In both *Squalus acanthias* (Ford, 1921) and *S. japonicus* (Chen *et al.* 1981) oocytes continue to develop

during gestation and females are able to mate soon after parturition and begin a subsequent cycle (Hanchet, 1988). Though such concurrent ovarian and uterine activity has been described in *Centrophorus niaukang* (Yano and Kugai, 1993) and *Centrophorus granulosus* (Capape, 1985) it is not a feature of any other deepwater squalid shark described to date (Girard and Du Buit, 1999; Yano, 1995; Yano and Tanaka, 1988) nor for the deepwater frilled shark *Chlamydoselachus anguineus* (Tanaka *et al.*, 1990). These authors speculate that the large livers in deepwater species leave little room in the body cavity for ripe oocytes during pregnancy. This seems a reasonable explanation, since deepwater sharks use their large livers to maintain neutral buoyancy (Corner *et al.*, 1969).

Species with well-defined female cycles generally display a predominance of certain reproductive stages at certain times of the year. Such cycles have been demonstrated for *Squalus acanthias* by Jones and Geen (1977c) and Hanchet (1988). In species such as this with a marked seasonality, it was quite easy to calculate the length of the gestation period. Its two-year gestation was first described by Ford (1921) off England and later by Templeman (1944) off Newfoundland. Elucidating the length of gestation period of other species has been less straightforward. Chen *et al.* (1981) tentatively concluded that *Squalus japonicus* had a one-year gestation period. However no deepwater squalid sharks described to date have displayed seasonal reproductive cycles (Girard and Du Buit, 1999; Yano, 1995; Yano and Tanaka, 1988) or for another deepwater species *Chlamydoselachus anguineus* (Tanaka *et al.*, 1990). These authors suggested that the absence of any seasonality in reproduction is hardly surprising since the deepwater environment is subject to so few hydrographic changes. No published information on gestation period exists for deepwater squalid sharks. However Tanaka *et al.* (1990) estimated that gestation in the frilled shark *Chlamydoselachus anguineus* may be 39 months based on measurements of embryonic growth rate in captivity.

1.4.3 Age and growth

Sustainable management of fish stocks requires a substantial body of information. An important component is knowledge of age. Data on age are used to estimate mortality and investigate growth of fish populations (Summerfelt and Hall, 1987). The first recorded study of age in fish was carried out by Hederstrom in 1759 using the vertebrae of pike *Esox lucius* (Ricker, 1975). For many years, age estimation has been carried out using scales, though in more recent years fin-spines, cleithra, otolith sections and opercular bones have also been used (Beamish and McFarlane, 1983). Many of these conventional age estimation techniques are not applicable to elasmobranchs, since they lack calcareous otoliths and other skeletal hard-parts (Cailliet *et al.*, 1983). Concentric growth bands were described from the vertebral centra of several elasmobranchs by Ridewood (1921). Since then centra have enjoyed the widest usage in elasmobranch age estimation studies, and many staining and sectioning techniques have been applied to these structures (Cailliet, 1990; Cailliet *et al.*, 1986). However several attempts to obtain age estimates from the vertebrae of squalid sharks were unsuccessful (Cailliet *et al.*, 1983; Polat and Gumus, 1995; Soldat, 1982) or the results were inconclusive (Jones and Geen, 1977a). Squalid sharks, in common with two other families Oxynotidae and Heterodontidae possess dorsal spines (Compagno, 1984; Maisey, 1979) and they were first used for age estimation by Kaganovskaia (1933) for spurdog *Squalus acanthias*.

Within the squalidae the *Squalus acanthias* has been the subject of most age estimation work. Early work was carried out by Kaganovskaia (1933) and Bonham *et al.* (1949) who counted the bands present on the surface of the spines. Later Holden and Meadows (1962) also considered the bands present in cross-sections. Cross-sections were also used by Soldat (1982), though Ketchen (1975), Nammack *et al.* (1985) and Polat and Gumus (1995) counted the marks on the surface. More recently attention has turned towards other squalid sharks and age estimation has been conducted for *Centrophorus acus* (Tanaka, 1990b), *Centrophorus granulosus* (Guallart Furio, 1998) and *Deania calceus* (Machado and Figueiredo, 2000).

Age estimate data are used to investigate growth. Several mathematical functions have been used to describe growth in length or weight with age. Among these are the von Bertalanffy, Gompertz and Logitsic models which form a family of growth functions

(Richards, 1959). Of these the von Bertalanffy model has enjoyed the greatest usage in elasmobranch biology. This is probably as a result of its application in the wider field of fisheries science where it has become incorporated into fisheries yield models (Beverton and Holt, 1957) and calculations of natural mortality (Pauly, 1980). However the Logitsic model was used in one recent elasmobranch growth study where the von Bertalanffy model did not adequately describe the data (Zeiner and Wolf, 1993).

While great progress was made on age estimation procedures in the early 20th century a study conducted by Beamish and McFarlane (1983) found that only 3 % of 500 works in this area proved that the estimates were accurate. These authors describe this determination of the accuracy of a technique as "validation". Accuracy can be proven or estimated, and in some instances only an estimate is possible (Beamish and McFarlane, 1983). These authors went on to state that validation is only complete when all age groups present in a fish population are validated. Despite the advances in age estimation in elasmobranchs, proof of annual band formation has only been accomplished for a small number of species. The most extensive study of any elasmobranch was conducted by Beamish and McFarlane (1985) on *Squalus acanthias*. However Holden and Vince (1973) were the first to validate age of an elasmobranch, the thornback ray *Raja clavata.* Later Smith (1984) showed that increments in the centra of leopard shark *Triakis semifasciata* formed annually. In other cases the results of tetracycline injection were less clear. Gruber and Stout (1983) were the first to display an annual periodicity in increment formation for the tropical lemon shark *Negaprion brevirostris*. But subsequent study of this species suggested a lunar periodicity (Brown and Gruber, 1988). Not all studies have found annual periodicity in band formation. Bands in the vertebrae of Pacific angel shark *Squatina californica* appeared to be related to somatic growth and not governed by any temporal periodicity (Natanson and Cailliet, 1990). Captive injections of Japanese wobbegong *Orectolobus japonicus* showed that in most cases increments formed annually (Tanaka, 1990a). However studies of gummy sharks *Mustelus antarcticus* showed that captive specimens deposited more increments over a given time period than wild specimens, probably due to laboratory-induced stress (Walker *et al.*, 1995) indicating the problems associated with captive studies.

While validation involves proving the accuracy of an age estimation method, the determination of precision of a set of estimates is termed verification (Wilson *et al.*,

1983). Two definitions of verification have been considered in the elasmobranch literature, that of Wilson *et al.* (1983) as the determination of precision and that of Cailliet *et al.* (1986) as a transitional stage in the process of determining the accuracy of a technique (validation). The process envisaged by Cailliet *et al.* is at an early stage for most elasmobranchs.

Detailed structural and ontogenetic descriptions of Squalidae fin-spines were produced by Maisey (1979). Maisey describes the spines of the Squalidae as having the same basic morphology. The exterior often possesses enamel ornamentation, though in some species this is much reduced in extent. The enamel and associated tissues overlie the main body of the spine, the trunk which is divided into two components viz. outer and inner layers (Maisey, 1979). The enamel in *Squalus acanthias* is characterised by a series of bands and ridges that formed the basis of several age estimation studies (Bonham *et al.*, 1949; Holden and Meadows, 1962; Kaganovskaia, 1933; Ketchen, 1972; Nammack *et al.*, 1985; Polat and Gumus, 1995).

Holden and Meadows (1962) considered the bands present on the surface of the spine to be an external reflection of the internal banding pattern, visible in cross-section. Subsequent work by Tucker (1985) appeared to indicate that the age estimates provided by Holden and Meadows (1962) were accurate. Validation of age was carried out successfully by McFarlane and Beamish (1987b) who used tetracycline mark and recapture methods. McFarlane and Beamish also described how the banding pattern forms; by a lack of synchrony between the upward growth of the trunk and the deposition of the cap at the base of the external spine. Slower growth of the trunk is not accompanied by a reduced secretion of cap enamelloid, leading to the ridges on the cap, visible as annuli (Beamish and McFarlane, 1985; McFarlane and Beamish, 1987b). By using tetracycline injection, these authors showed that the bands present on the surface were annual in formation. It also became clear that the banding visible in cross-section was not associated with the surface pattern. While the bands in the cross-section were not associated with those on the surface, they were found to be annual in formation also (McFarlane and Beamish, 1987b). It became clear from the results of this study that *Squalus acanthias* was longer lived and later maturing than previously thought.

An important conclusion of McFarlane and Beamish's (1987b) was that there was no reason to group or otherwise reject certain bands that were considered to be sub-annual. All bands present on the surface of the spine of *Squalus acanthias* were annual and therefore should be considered in counts of bands (Beamish and McFarlane, 1985). The disadvantage in using an organ such as the dorsal spine which is external to the body of the fish is that it is subject to wear. Ketchen (1975) calculated a spine base diameter-age estimate regression for unworn spines to estimate the age of a given fish. While this method relies on an assumption of constant growth and may lead to errors it was considered the only means to correct age estimates for worn spines (McFarlane and Beamish, 1987b).

McFarlane and Beamish's (1987b) finding that there was no basis for grouping of bands has important implications for future studies of age in Squaliform sharks. Underestimation of age results in an overestimation of mortality rate and may lead to over-optimistic predictions about yield from a fishery (Beamish and McFarlane, 1983). However there has only been one age study of *Squalus acanthias* conducted subsequent to McFarlane and Beamish's validation study, that of Polat and Gumus (1995) in the Black Sea. Nevertheless age estimates of *Squalus acanthias* have formed the basis of several demographic studies. Ketchen's (1975) age estimates from the NE Pacific were used in a subsequent population model by Wood *et al.* (1979) while those of Nammack *et al.* (1985) was used by Rago *et al.* (1998) in constructing a population model for the NW Atlantic stock.

Age estimation studies of other Squalidae have been based on cross-sectional bands. This is because these species do not have the extensive surface enamel possessed of *Squalus acanthias*, as described by Maisey (1979). There have been differing interpretations of the internal morphology of spines with some authors such as Holden and Meadows (1962) and Tanaka (1990b) considering three internal dentine zones, while others (Guallart Furio, 1998; Machado and Figueiredo, 2000) considered two as described by Maisey. However the study of Maisey (1979) and the findings of McFarlane and Beamish (1987b) formed the basis of the age estimation component of the present study.

1.4.4 The impacts of fishing

Elasmobranchs have been evolving independently for at least 450 million years (Hoenig and Gruber, 1990). Typically, they are slow growing, long-lived and mature at advanced age (Bonfil, 1994). Furthermore the majority of species have low fecundities, and while there may be some scope for increases in litter sizes as stocks decline (Holden, 1974) the maximum number of young produced is considered to be strictly limited (Hoenig and Gruber, 1990). The life history strategies of most elasmobranchs suggest that they cannot sustain high levels of directed fishing pressure (Holden, 1973). Nonetheless, elasmobranchs are now subject to greater reductions than at any time in their long history (Heuter, 1998). As a result of commercial exploitation, global landings reached an estimated 800,000 tonnes by 1998 (FAO, 1998a). Despite these increases the knowledge base for most exploited elasmobranch populations is limited. A review of world elasmobranch fisheries cited the lack of important baseline information as an impediment for fisheries assessment (Bonfil, 1994). Bonfil noted that in the light of these considerations it was not surprising that elasmobranch fisheries have often proved unsustainable.

The history of shark fisheries has been described as one of "boom and bust" (Pratt and Casey, 1990). This trend has been described from the Irish basking shark fishery (Kunzlik, 1988 and references therein), Irish spurdog fishery (Fahy, 1992) fisheries for pelagic sharks off California (Cailliet and Bedford, 1983) and the soup-fin shark fishery off Australia (Olsen, 1954). However little documentary evidence on the status of deepwater shark fisheries exists (Gordon, 1999). While Yano and Tanaka (1984) state that a long-line fishery for deepwater sharks has operated since the 1940s in Suruga Bay, Japan, there is no published information on the status of these shark stocks. While declining landings of *Dalatias licha* at the Azores (Anon, 2000b) may be due to decreasing biomass, Gordon (1999) suggested that it may reflect fluctuations in the price of liver oil. Declining Catch per Unit Effort (CPUE) of squalid sharks from French trawlers in the Rockall Trough was reported by Lorrance and Dupuoy (1998). This CPUE series combined catch data for *Centrophorus squamosus* and *Centroscymnus coelolepis*, the two commercial species. Gordon (1999) reflecting on this study suggested that the squalids were more resilient to fishing pressure than the other (teleost) species, and speculated that their wide-ranging distributions were probably the reason.

However, in Australia marked declines in CPUE for squalid sharks have been described by Graham (1997).

Shark fisheries worldwide are prosecuted using a variety of gears. The principal methods are gill-nets, drift nets, long-lines, trawls and purse seines (Bonfil, 1994). Fisheries for deepwater sharks are mainly based on drop-lines (Silva, 1988); long-lines (Iglesias and Paz, 1995; Pineiro *et al.*, 1998) and trawls (Charau *et al.*, 1995). However little information exists on the relative catching efficiencies of these gears for sharks, or their selective properties. While Jørgensen, (1995) compared trawl and long-line catching efficiencies for Greenland halibut *Reinhardtius hippoglossoides* no similar work exists for deepwater sharks. Bait size has been cited as the most important parameter in size selectivity of long-lines for teleosts since smaller fish tend to favour prey below a certain size (Bjordal and Lokkeborg, 1996). While Branstetter and Musick (1983) investigated the catching efficiencies of long-lines with different snood-types, no information exists on the size selective properties of long-lines for sharks. Similarly the selectivity of trawls for sharks is poorly understood. Gordon (1999) felt that headline height may influence species composition and catch rates. It seems unlikely that mesh size would have any selective effects for deepwater sharks as experiments showed that very small *Coryphaenoides rupestris* of 3 cm pre-anal fin length were retained by commercial (105 mm) cod-ends (Kelly *et al.*, 1998).

Discarding of fish at sea has been recognised by fisheries scientists as an inherent problem in the management of fisheries world-wide. Discards are defined as that part of the catch returned to the sea while the term by-catch refers to discarded catch plus incidental catch (Alverson *et al.*, 1994). It is known that sharks are a by-catch in many fisheries worldwide, though little information exists on the actual quantities discarded (Bonfil, 1994). Bonfil reviewed existing data though little information on deepwater sharks was presented. A study of the subject, in the Rockall Trough trawl fishery showed that *Deania calceus* and *Centroscymnus crepidater* accounted for the greatest weight among discarded species (Connolly and Kelly, 1996). Discards of *Deania calceus* in the New Zealand deepwater fishery may account for 20 % – 50 % of orange roughy catch (Bonfil, 1994). Further work by Blasdale and Newton (1998) found that the discard rates of *Deania calceus* from different trawl nets were not greatly different. It

seems unlikely that many discarded deepwater sharks could survive owing to damage, stress and pressure changes (Gordon, 1999).

The life-history strategies of elasmobranchs suggest that they may not support directed fisheries (Holden, 1974). While density-dependent increases in fecundity may be possible in some species (Holden, 1973) the limit of absolute number of progeny must be fixed (Hoenig and Gruber, 1990). These authors discuss the implications of life-history strategies. In addition to age, growth and reproductive characteristics they cite movements such as migration, dispersal and social segregation as traits with important implications for shark fisheries management. Large scale trans-Atlantic migrations have been described for *Squalus acanthias* (Templeman, 1976) and pelagic species (Kohler *et al.*, 1998), but not for deepwater species. However the absence of smaller specimens in many areas (Section 1.4.1) may indicate that these species undergo movements as postulated by Yano and Tanaka (1984).

The FAO International Code of Conduct for Responsible Fisheries (FAO, 1996) requires that states take a precautionary approach to fisheries management and that lack of adequate data should not be a deterrent to implementing such plans. Elasmobranchs are receiving increased international research interest and have become the focus of recent initiatives to secure their sustainability through effective management. The FAO, international action plan for the conservation and management of sharks (FAO, 1998b) is of particular relevance in this regard, specifically recognising the need for better management of directed elasmobranch fisheries and certain multi-species fisheries in which sharks constitute a significant bycatch.

Table 1.3. Available information on the species under study.

Centroscymnus coelolepis Bocage and Capello, 1864	
Common names	foca (Castillian Spanish), gata (Gallego), corrocho (Portuguese), siki (French), Portuguese dogfish (English), dypvannshå (Norwegian)
Distribution	Bridger, 1978; Cadenat and Blache, 1981; Carasson *et al*. 1992; Clark and King, 1989; Compagno, 1984; Ebert *et al*., 1992; Forster *et al*., 1970; Gordon and Swan, 1997; Hareide and Thomsen, 1987; Yano and Tanaka, 1983a and b; 1984; 1988
Reproduction	Girard and DuBuit, 1999; Yano and Tanaka, 1987
Age and growth	None
Diet	Carasson *et al*., 1992; Ebert *et al*, 1992; Mauchline and Gordon, 1983
Fisheries	Charuau *et al*., 1995; Gordon, 1999; Iglesias and Paz, 1995; Pineiro *et al*., 1998; Yano and Tanaka, 1984
Centrophorus squamosus (Bonnaterre, 1788)	
Common names	Cochon (French), lixon (Gallego), lixa (Portuguese), lija (Castillian Spanish) leafscale gulper shark (English), brunhå (Norwegian)
Distribution	Bridger, 1978; Cadenat and Blache, 1981; Compagno, 1984; Forster *et al*., 1970; Gordon and Swan, 1997; Hareide and Thomsen, 1987; Yano and Tanaka 1983
Reproduction	Girard and Du Buit, 1999
Age and growth	None
Diet	Ebert *et al*., 1992
Fisheries	Charuau *et al*., 1995; Gordon, 1999; Iglesias and Paz, 1995; Mauchline and Gordon, 1983; Yano and Tanaka, 1984
Deania calceus (Lowe, 1839)	
Common names	Pala (Gallego), sapata (Portuguese), visera (Castillian Spanish), squale savate (French), birdbeak dogfish (English, England), shovelnose spiny dogfish (English, New Zealand), gråhå (Norwegian)
Distribution	Bridger, 1978; Cadenat and Blache, 1981; Clark and King, 1989; Ebert *et al*., 1992; Gordon and Swan, 1997; Hareide and Garnes, 1998; Yano and Tanaka, 1983 a and b.
Reproduction	None
Age and Growth	Machado and Figueiredo, 2000
Diet	Clark and King, 1989; Ebert *et al*. 1992; Mauchline and Gordon, 1983; McPherson and Roel, 1987; Yano, 1991
Fisheries	Bonfil, 1994; Gordon, 1999; Iglesias and Paz, 1995; Pineiro *et al*., 1998; Yano and Tanaka, 1984

1.4.5 The Species under study

1.4.5.1 *Centroscymnus coelolepis* Bocage and Capello, 1864

Centroscymnus coelolepis (Fig. 1.6) is distinguishable from other members of its genus by the short snout, which is about 2/3 the distance from mouth to first gill slits, and less than the mouth width. The lateral trunk denticles are very large, with smooth rounded crowns in adults. The body does not taper from the pectoral fins, the first dorsal fin-base is not extended forwards and is well behind the pectorals (Compagno, 1984). Originally, it was thought to be found only in the Atlantic, where it occurs in the east from the Azores and Madeira north to Iceland, and in the west from the Delaware Bay north to the Grand Banks (Compagno, 1984) (Fig. 1.7). It has also been recorded from Norfolk Canyon (Musick and Gelsleighter, *pers. comm.*). Compagno (1984) speculated on its occurrence in the western Pacific and New Zealand. Yano and Tanaka (1983b) confirmed its presence off Japan, and Clark and King (1989) recorded it from New Zealand. Hareide and Thomsen (1997) caught this species on the Mid-Atlantic Ridge north of the Azores and south of Iceland, but not on the Hecate or Faraday Seamounts.

It is stated to occupy depths from 270 m – 3,675 m (Compagno, 1984). In Suruga Bay, Yano and Tanaka (1983a) recorded it in the range 300 m – 1,200 m. Ebert *et al.* (1992) caught this species at all depths fished (660 – 1,016m) off Namibia, however it probably occurs in deeper waters also. Gordon and Swan (1997) recorded its entire depth range as lying between 366 m and 1,750 m. This species appears to segregate according to reproductive state. Yano and Tanaka (1988) found gravid females in shallower waters than immature specimens in Suruga Bay, Japan. There was evidence, from this area, of segregation within the genus, with *C. owstoni* occurring in shallower waters (Yano and Tanaka, 1984). Its congener in the north-east Atlantic, *C. crepidater* occurs in shallower waters too (Gordon and Swan, 1997). Nevertheless it seems unlikely that this is due to dietary preferences since the latter species feeds on micro-nekton while *Centroscymnus coelolepis* in this area was reported as a consumer of demersal fish (Mauchline and Gordon, 1983).

Mauchline and Gordon's (1983) designation of *Centroscymnus coelolepis* as a consumer of demersal fish concurs with Compagno (1984). However, Clarke and Merrett (1972)

found that cephalopods were the commonest prey items. These authors also found skin and blubber, tentatively identified as from sperm whales *Physter catodon* and speculated that this might indicate a scavenging behaviour, though they did not rule out the possibility that it attacks such fast moving prey.

Yano and Tanaka (1984) and Girard and Du Buit (1999) both noted the absence of smaller specimens from Suruga Bay, Japan, and the northeast Atlantic respectively. However a complete inventory of sizes was reported by Ebert *et al*. (1992) off Namibia. No published information on age or growth is available for this species. There are two studies of reproduction in this species. Yano and Tanaka (1987) described the anatomy and morphology of male and female reproductive systems. They note that while embryos may obtain some nutrients from the villi, they are mainly yolk-dependent. The species conforms to the aplacental viviparous type II classification of Otake (1990) (Girard and Du Buit, 1999). These authors conducted a study of reproduction in the northeast Atlantic. They reported ovarian fecundity of 8 –22 and uterine fecundity of 8 - 19. Length at 50 % maturity was estimated as 86 cm and 102 cm for males and females respectively. Fecundity in Suruga Bay was 23-24 (ovarian) and 15-29 (uterine). Lengths at 50 % maturity in Japan were attained in the range 70 cm – 75 cm by males and 95 cm - 99 cm range for females (Yano and Tanaka, 1988). Neither study found any evidence of a seasonal cycle in reproduction.

This species, along with *Centrophorus squamosus* is an important by-catch in the mixed-species deepwater trawl fishery west of Scotland and Ireland (Charuau *et al.*, 1995). It is also targeted by Spanish-owned long-liners in this area and southwards along the continental slopes to the north coast of Spain (Iglesias and Paz, 1995; Pineiro *et al.*, 1998). Several artisanal long-line fisheries take this species on the continental slopes of Portugal (EC FAIR, 1999) and at Madeira and the Azores (Anon, 2000b). A fishery for members of this genus has been in operation in Suruga Bay, Japan since the 1940s (Yano and Tanaka, 1984). *Centroscymnus coelolepis* is probably taken in high-seas fisheries in the north Atlantic by Spain, Russia and other eastern European countries, though data are lacking.

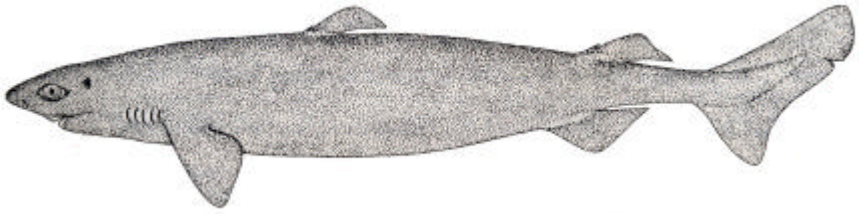


Fig. 1.6. *Centroscymnus coelolepis* Bocage and Capello, 1864, redrawn from Compagno (1984).

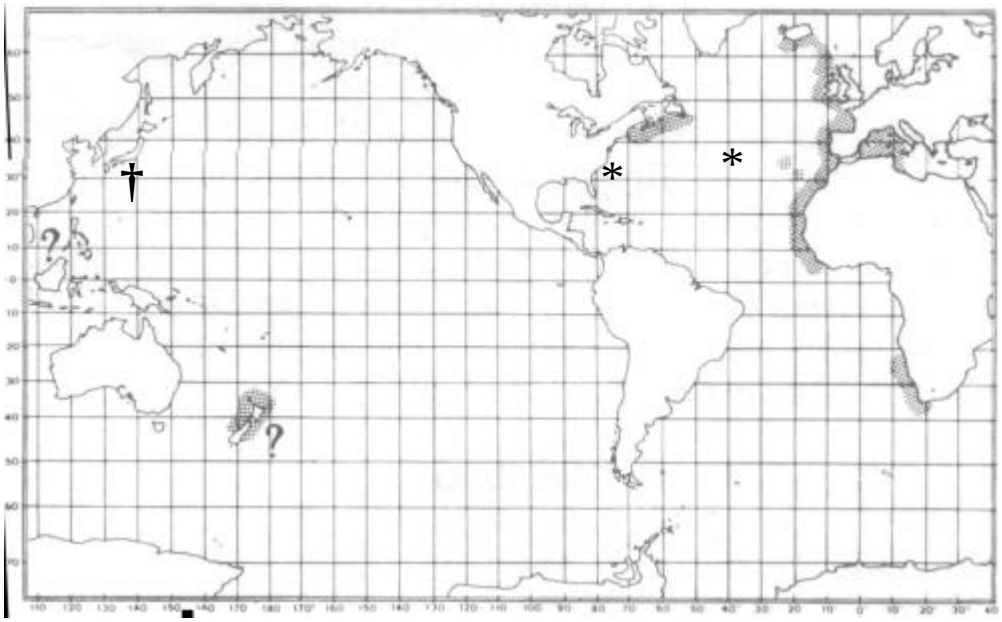


Fig. 1.7. Distribution map of *Centroscymnus coelolepis* redrawn from Compagno (1984) with the following additions;

† Presence in Japanese waters confirmed by Yano and Tanaka (1983b).

* Also present on the Mid-Atlantic Ridge (Hareide and Garnes, 1998) and Norfolk Canyon, off Virginia, USA (Musick and Gelsleighter *pers. comm*.).

1.4.5.2 *Centrophorus squamosus* (Bonneterre, 1788)

Centrophorus squamosus (Fig. 1.8) is distinguishable from congeners by having dermal denticles with multiple lateral cusps and leaf-like flattened crowns on elevated, narrow to broad pedicles. The free rear tips of the pectoral fins are broadly angular, not extending behind the first dorsal fin (Compagno, 1984). Compagno considers his 1984 key for the genus *Centrophorus* to be "highly tentative" and there have been recent revisions of the genus (Compagno 1999a and b; Guallart Furio, 1998; Muñoz-Chapuli and Ramos, 1989) concerning those congeners with sessile, block-like denticles. However *Centrophorus squamosus* (*sensu* Compagno, 1984 and McEachran and Branstetter, 1984), with denticle crowns elevated on pedicles, is not subject to this controversy. It occurs in the Atlantic Ocean from Iceland to Senegal, the Azores, Madeira, Gabon to Zaire and the Cape coast of Africa. It is also found in western Indian Ocean, the Phillipines, Japan, southeastern Australia and New Zealand (Compagno 1984), see Fig. 1.9. It was recorded along with an unidentified congener in the western Indian Ocean (Forster *et al.* 1970) and is also present on the Faraday Seamount and Reykjanes Ridge areas of the Mid-Atlantic Ridge (Hareide and Garnes, 1998). Bridger (1978) felt that in addition to this species two other members of the genus were present west of Ireland and Britain, tentatively assigning some specimens to *Centrophorus uyato* and *C. granulosus.* The presence, in this area, of *Centrophorus uyato* (*sensu* Compagno, 1984) was noted by Clarke (2000).

Members of the genus *Centrophorus* in Suruga Bay, Japan, displayed a marked segregation, with *C. atromarginatus* occurring in shallowest waters, *C. squamosus* in the deepest waters (greater than 800 m) and *C. acus* occupying the middle depths (Yano and Tanaka, 1983a). Compagno (1984) considered *Centrophorus squamosus* a dogfish of continental slopes from 229 m – 2,359 m agreeing with Bridger's (1978) finding that it was much less abundant on the off-shore banks than on the slopes west of Ireland and Britain. Though reported to be rare in depths less than 1,000 m in the eastern Atlantic (Compagno, 1984), peak abundance was recorded in the Rockall Trough by Gordon (1999) at about 900 m.

Lengths attained are reported as up to 158 cm, males maturing at 103 cm and females at 137 cm to 158 cm (Compagno 1984). A complete size range for this species was reported by Ebert *et al.* (1992) and Yano and Tanaka (1983a) reported specimens as

small as 481 mm from Suruga Bay, Japan. However, other authors reported missing smaller sizes of this species; Hareide and Thomsen (1997) for the Mid-Atlantic Ridge and Girard and Du Buit (1999) west of Ireland and Britain.

Little information exists on the diet of this species. Cephalopods were found to be the dominant prey group of this species off southwest Africa, followed by several species of teleosts by Ebert *et al.* (1992). Information on reproduction in this species is also limited. The species is ovoviviparous, producing litters of 5 embryos according to Compagno (1984). While gravid females were absent from their area of reference Girard and Du Buit (1999) reported that mean ovarian fecundity was 10 and that the species conforms to the aplacental viviparous type II classification of Otake (1990). Length at 50 % maturity was estimated as 98 cm and 124 cm (Girard and Du Buit, 1999). No information exists on age or growth in this species.

This species, along with *Centroscymnus coelolepis* is an important by-catch in the mixed-species deepwater trawl fishery west of Scotland and Ireland (Charuau *et al.*, 1995). It is also targeted by Spanish-owned long-liners in this area and southwards along the continental slopes to the north coast of Spain (Iglesias and Paz, 1995; Pineiro *et al.*, 1998). Several artisanal long-line fisheries take this species on the continental slopes of Portugal (EC Fair, 1999), Madeira and the Azores (Anon, 2000b). A fishery for members of this genus has been in operation in Suruga Bay, Japan since the 1940s (Yano and Tanaka, 1984). *Centrophorus squamosus* is caught in high-seas fisheries in the north Atlantic by Spain (Duran *et al.*, 2000), and probably Russia and other eastern European countries, though data are lacking.

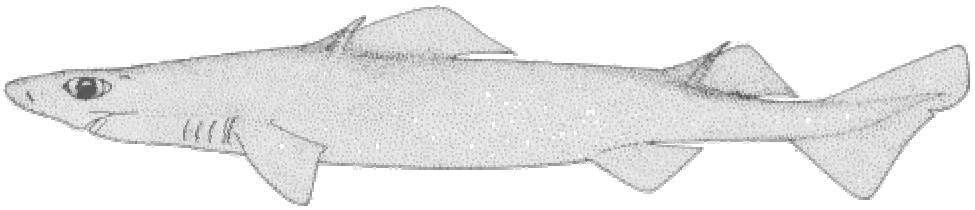


Fig. 1.8. *Centrophorus squamosus* (Bonnaterre, 1788), redrawn from Compagno (1984).

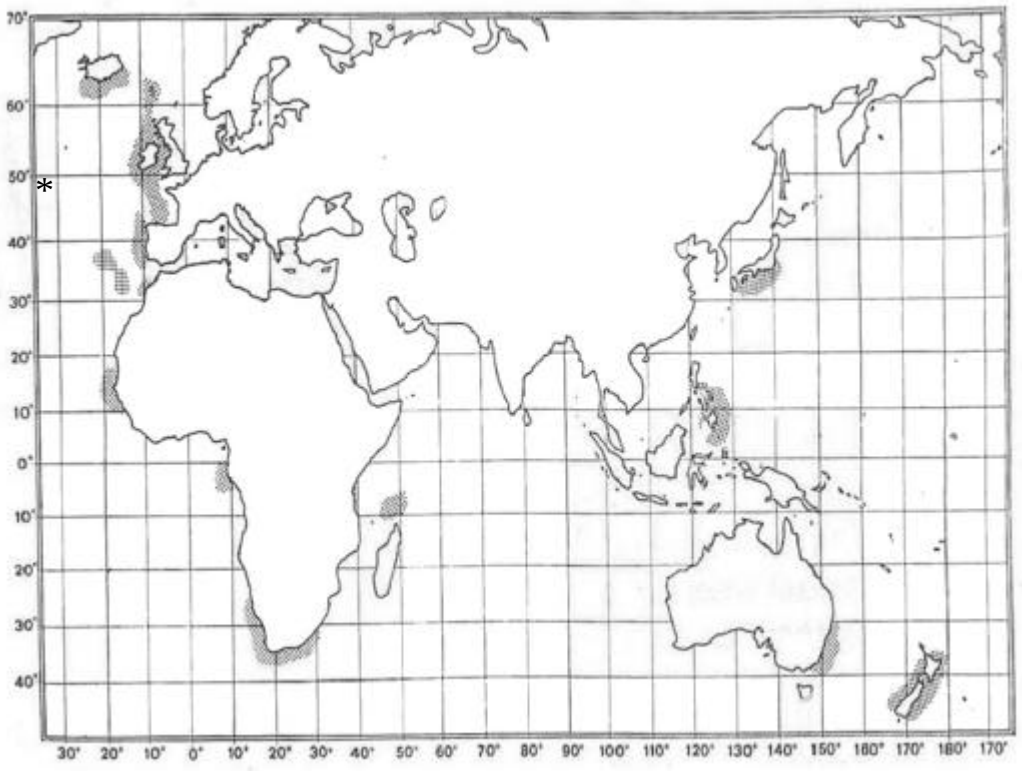


Fig. 1.9. Distribution of *Centrophorus squamosus*, redrawn from Compagno (1984) with the following addition;

* Also present on the mid-Atlantic Ridge (Hareide and Garnes, 1998).

1.4.5.3 *Deania calceus* (Lowe, 1839)

This species (Fig. 1.10) is distinguishable from congeners by the absence of a sub-caudal keel, low, long and rounded first dorsal fin, the distance of its spine origin to free rear tip greater than from free rear tip to second dorsal spine origin. The lateral trunk denticles are moderately large, with crowns about 0.5 mm long (Compagno, 1984). It is found in the eastern north Atlantic from Iceland to west Africa, the Faroes, Madeira, Namibia, Chile, New Zealand, south Australia and Honshu (Japan) (Compagno 1984), see Fig. 1.11. It is also found on the Reykjanes Ridge and the Faraday Seamount areas of the Mid-Atlantic Ridge, though not on the Hecate Seamount (Hareide and Garnes, 1998). A congener, *Deania histricosa* (*Deania mauli, sensu* Cadenat and Blache, 1981) also present in the north Atlantic, is distinguishable from by having larger lateral trunk denticles, about 1mm long (Compagno, 1984).

Compagno (1984) reports a depth range of 73 m – 1,450 m, though other authors have not recorded it in such shallow waters. Ebert *et al.* (1992) found it in the range 475 m to 900 m and Yano (1991) in 620 – 644 m off southwest Africa. In the northeast Atlantic Gordon (1999) found peak abundance between 500 and 1,000 m. *Deania calceus* was considered to segregate by size and sex by Clark and King (1989) who suggested that it undergoes extensive migrations around North Island New Zealand. A segregation by depth between this species and its congener *D. rostrata* was reported by Yano and Tanaka (1983a) who noted that while their depth ranges overlapped in shallow water (150 m – 350 m), *D. calceus'* range extended deeper than 800 m.

In the Rockall Trough *Deania calceus* was found to prey mainly on demersal fish (Mauchline and Gordon, 1983). However myctophids were the dominant prey item, followed by cephalopods off Namibia (Ebert *et al.*, 1992; Yano, 1991) and off New Zealand (Clark and King, 1989). Bridger (1978) recorded the epi-pelagic teleosts; scad *Trachurus trachurus* and mackerel *Scomber scombrus* in stomachs of this species, suggesting that it undergoes extensive vertical migrations. Such movements may explain Compagno's (1984) statement that this species is caught in mid-water trawls in the eastern Atlantic. However it may prey on meso-pelagic species because of their lateral impingement on the slopes, while diurnal vertical migrations of epi-pelagic species may account for their presence in its diet. These feeding relationships have been described for

other deepwater organisms by Mauchline and Gordon (1991). Mauchline and Gordon (1983) suggested that it feeds at some distance from the seabed. Its elongated snout suggests an enhanced ampullary system and the posterior position of the dorsal fins and the paddle-like pectorals, a high degree of manoeuvrability in the vertical plane (Tabit, 1993). These adaptations may indicate mid-water habits. MacPherson and Roel (1987) did not find any evidence for ontogenetic changes in prey preferences of specimens in the range 40 – 110 cm TL off Namibia.

Maximum size is reported as 111 cm (Compagno 1984). Yano and Tanaka (1983) report a full size range (31 cm – 121 cm) TL was taken from Suruga Bay. However off Namibia Ebert *et al*. (1992) did not find any specimens smaller than 55 cm. Working in the same area, Yano (1991) did not record specimens smaller than 45 cm.

There is little published information on reproduction in this species. Clark and King (1989) found a predominance of late-term females in one area off North Island New Zealand and suggested that they may form breeding aggregations in this area. These authors found that only one quarter of females were reproductively active, and felt this may indicate a four-year resting period. Compagno (1984) speculated that it may produce 6-12 young, based on ovarian fecundity data. Yano (1991) counted 19 ova in an immature female. The only age estimation study is the recent work of Machado and Figueiredo (2000) for Portugal. Histological cross-sections were used to produce age estimates for specimens from 25 cm up to 86 cm.

Deania calceus is taken by Spanish-owned long-liners on the continental slopes from Scotland southwards to the north coast of Spain (Iglesias and Paz, 1995; Pineiro *et al.*, 1998), though only the liver is retained (Mulligan, 2000). It is discarded by trawlers in the mixed-species fishery west of Ireland and Britain (Connolly and Kelly, 1996). The livers have been the basis of a fishery in Suruga Bay, Japan since the 1940s (Yano and Tanaka, 1984). This species accounts for between 20 % and 50 % of the catch in the New Zealand target fishery for orange roughy *Hoplostethus atlanticus* and consequently between 4,400 and 22,000 tonnes of this species may be caught every year in that area (Bonfil, 1994). This level of fishing is above maximum sustainable yield as calculated by King and Clark (1987). Compagno (1984) states that it is caught in mid-water trawls, though there is no evidence for this exists.

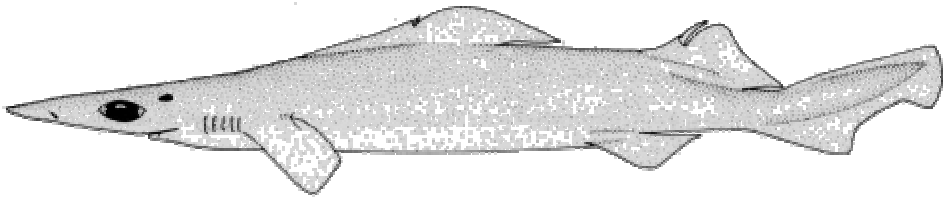


Fig. 1.10. *Deania calceus* (Lowe, 1839), redrawn from McEachran and Branstetter (1984).

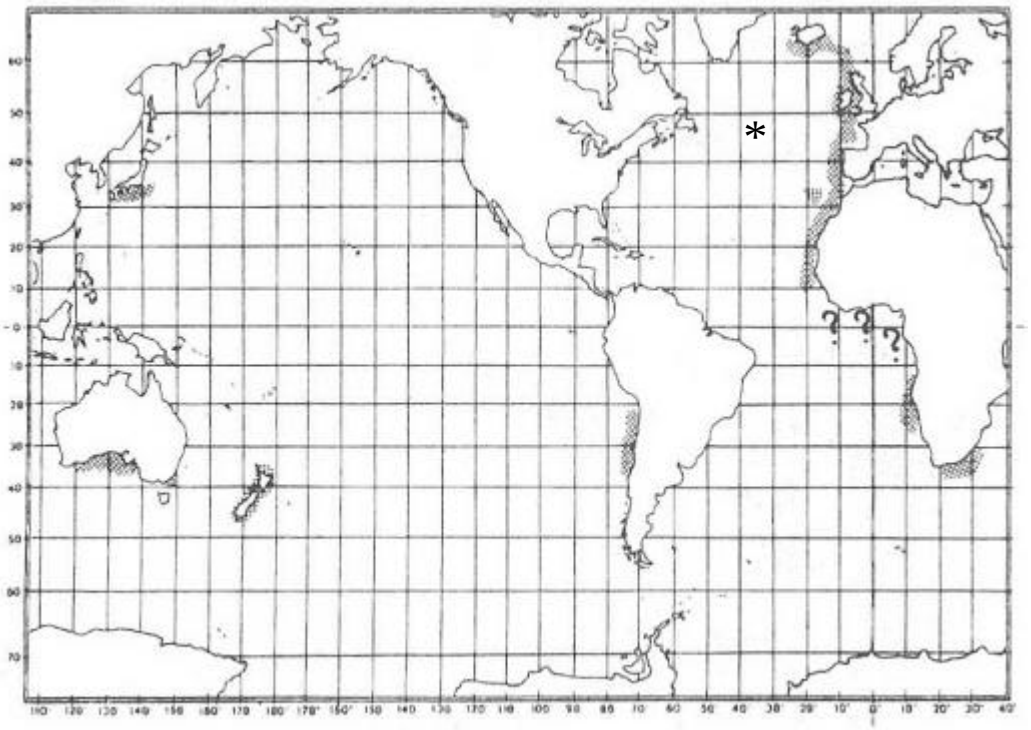


Fig. 1.11. Distribution of *Deania calceus* redrawn from Compagno (1984) with the following addition;
* Occurs on the Mid-Atlantic Ridge (Hareide and Thomsen, 1997).

1.5 The scope and purpose of this study

Deepwater squalid sharks are heavily exploited at present in the Rockall Trough and Porcupine Bank, and with only limited management measures in place. Concerns have already been expressed about sustainability (Hopper, 1995). Of the squalid sharks present in these areas *Centrophorus squamosus* and *Centroscymnus coelolepis* are routinely landed, though separate landings data for each species are unavailable. The remainder of the species are discarded, and early studies have shown that *Deania calceus* is the dominant discard species (Connolly and Kelly, 1996). These three species were chosen for study because they are the most abundant squalid sharks in trawl and long-line catches (Connolly and Kelly, 1996) and because little biological information exists to enable fishery management plans to be developed (Hopper, 1995). The almost prohibitive cost of conducting research programmes in deepwater, especially for individual countries, has been recognised. In order to maximise the benefits of such research programmes the Commission of the European Communities, in 1996, awarded a 3-year contract to a consortium of twelve national fisheries research institutes to increase the knowledge base required for rational management of deepwater fish stocks. In Ireland the Marine Institute was tasked to analyse the data from the survey programme underway since 1992 and to establish the biological parameters of exploited species (EC FAIR, 1999). This work represents a part of the Irish contribution to that study.

The main objective of this study was to contribute to the biology of these species in order to permit some informed decisions to be made about the effects of the fisheries. Information on reproduction is central to studies of exploited shark populations (Pratt and Otake, 1990. Among biological parameters of the three species under study, were size at maturity, fecundity and reproductive cycle. An explicit aim was to establish if there was any periodicity in the reproductive cycles of theses species.

Investigations of growth in fish populations are often based on age information (Summerfelt and Hall, 1987). However, there are few studies of age in deepwater sharks and none have been validated (Gordon, 1999). The usefulness of dorsal spines and centra for determining age in these species was investigated. Cailliet et al. (1986) recommends that age estimation techniques should be developed and verified as a step towards obtaining accurate age data for elasmobranch species. As a first step towards

obtaining accurate age estimates, the usefulness of dorsal spines and vertebral centra for age estimation were investigated and the precision of band counts tested.

The main fishing gears used in the deep waters north and west of Ireland are trawls and long-lines. It is known that these gears have different selective properties (Hareide, 1995) and yet little information exists on the differing sizes of squalid sharks taken by each method. The size selectivity of a fishing method will determine its effect on the species in the catch. An objective of this study was to investigate the selectivity parameters for these squalid sharks. Research surveys by trawl and long-line were the basis of this work. It is known that squalid sharks segregate by size and sex (Wetherbee, 1996; Yano and Tanaka, 1988). By fishing in different depth strata in fixed areas along the continental slopes of the Rockall Trough and Porcupine Bank the distribution and abundance of the three species has been documented.

Landings data for deepwater sharks are not species specific so it is difficult to identify trends in shark catches. While limited information is available for *Centrophorus squamosus* and *Centroscymnus coelolepis*, the situation for *Deania calceus* is more problematic. In spite of its dominance in catches in this area (Connolly and Kelly, 1996) it is discarded at sea, with the liver being retained in some cases. Estimates of the quantities of this species discarded are presented. Since it seems unlikely that discards would survive (Kelly *et al.*, 1998) the effects of this practice on the population structure and on the ecosystem are discussed.

The study provides base-line information on three exploited squalid sharks. It represents a contribution to the information that is required for rational management decisions as envisaged by Hopper (1995). This information is discussed against the backdrop of increasing and diversifying fishing pressures. The deficiencies in the knowledge base are highlighted and some conclusions as to the effects of the fisheries and potential management regimes are advanced.

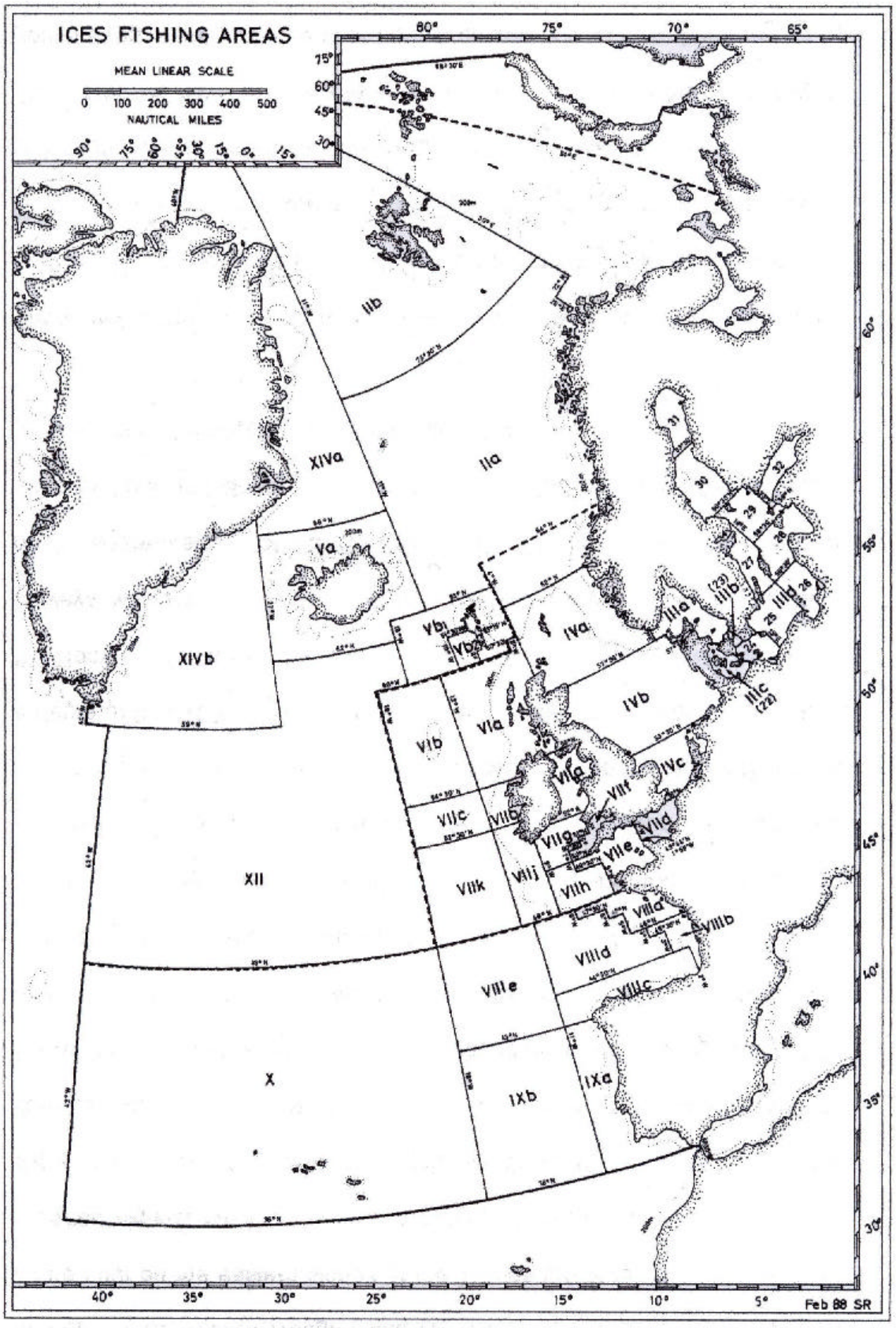


Fig. 1.12. Fishing areas used by the International Council for the Exploration of the Sea (ICES). The study area comprises the deepwater slopes of Sub-Areas VI and VII.

Plate 1.1. One of the large French deepwater trawlers landing catch at Lochinver, Scotland in June 1998. A fleet of these vessels targets deepwater species west of Scotland and Ireland but also fish on the continental shelf for saithe *Pollachius virens*.

Plate 1.2. Some of the fleet of smaller French deepwater trawlers at Concarneau, France in April 1997. These vessels target deepwater species, including squalid sharks, but also fish for shelf species such as hake *Merluccius merluccius*, monk-fish *Lophius* and megrim *Lepidorhombus*.

2 Materials and methods

2.1 General Procedures

Samples for this project were secured from two sources, research surveys (fishery independent) and commercial landings (fishery dependent) (Clarke *et al.*, 1999; Connolly *et al.*, 1999; Kelly *et al.*, 1998). The Marine Institute began sampling surveys in the deep waters of the Rockall Trough and Porcupine Bank in 1993. Samples for the present study were collected on these surveys from November 1995 onwards. In total three otter trawl and three bottom-set long-line surveys were conducted in this period (Table 2.1). An inventory of samples of the three species under study is presented in Table 2.2.

The purpose of these surveys was to obtain samples of deepwater fish, crustaceans and cephalopods for biological, chemical and food-technology analysis by the Marine Institute. In addition those surveys carried out from 1996 onwards provided important information on catch rates and distributions of deepwater sharks. The trawl surveys were carried out on board the trawler *Mary M* (Plate 2.1).

The first long-line survey (November/December 1995) was conducted using the *Sea Sparkle*, a converted trawler (Plate 2.2). The second long-line survey, carried out in August 1997, was carried out on the long-liner *Skarheim* of Norway. A second Norwegian vessel, the *Loran*, was used for the third long-line survey in November and December 1999 (Plate 2.3). In order to minimise costs, the vessel owners retained and sold the catch as part of the charter agreement. Samples from commercial trawlers were obtained at Lochinver in Scotland (Table 2.3) where deepwater trawlers working in the Rockall Trough land their catches.

Table 2.1. Details of trawl and long-line surveys from which samples and information for this project were obtained.

Vessel	Type	No. of Hauls	Month and Year	Depths (m)
Mary M	Trawl	26	November, 1995	740-1400
Sea Sparkle	Long-line	22	November/December 1995	542-1332
Mary M	Trawl	26	September, 1996	560-1102
Skarheim	Long-line	32	August, 1997	292-2925
Mary M	Trawl	22	October/November 1997	520-1158
Loran	Long-line	38	December, 1999	514-1974

Table 2.2. Samples of all deepwater shark material obtained.

Species	Organ	Preservative	Number
Centrophorus squamosus	Gonad	4 % Buffered Formalin	462
	Centra/Spine	70 % Alcohol	476
	Spine	70 % Alcohol	104
Centroscymnus coelolepis	Centra/spine	70 % alcohol	358
	Gonad	4 % Buffered Formalin	356
Deania calcea	Centra/spine	70 % Alcohol	406
	Gonad	4 % Buffered Formaldehyde	301

Table 2.3. Samples of deepwater sharks obtained (fishery dependent) at Lochinver, Scotland, 1997/1998.

Sample	*Centrophorus squamosus*	*Centroscymnus coelolepis*
1st Quarter	27 Spines	101 Spines
March 1997	27 Centra	101 Spines
	27 Gonads	101 Gonads
2nd Quarter	10 Spines	102 Spines
June 1998	0 Centra	0 Centra
	10 Gonads	102 Gonads
3rd Quarter		98 Spines
July 1997		0 Centra
		98 Gonads
4th Quarter	63 Spines	97 Spines
December 1997	0 Centra	0 Centra
	63 Gonads	63 Gonads

Specimens of sharks were identified according to Compagno (1984) and McEachran and Branstetter (1984). Total length was considered to be the length from the snout tip to the posterior tip of the caudal fin depressed along the anterior-posterior axis. This measurement was recorded to the nearest centimetre below the actual length of the fish. Round weight - and where possible gutted and liver weights (g) - and sex were recorded. Spines were removed by cutting towards the notochord. First and second dorsal spines were placed in Sterilin® tubes and preserved in 70 % alcohol. The entire spine was not always removed as this had a detrimental effect on the marketability of the sharks. Vertebral centra were removed from beneath the first dorsal fin by making two incisions along the vertebral column. From each shark 4 or 5 centra were removed and stored in labelled Sterilin® tubes in 70 % alcohol. Data were recorded on customised record sheets, see Appendix I for formats used. Gonads were excised from the sharks and stored in labelled tubes, 12 oz. jars or museum jars in 4 % buffered formaldehyde. Embryos (pups) were also stored in formaldehyde or frozen in

labelled bags. Measurements of some morphological characters were taken using a 0.1mm dial calliper. These measurements were: testes width; largest ovarian egg diameter; second largest ovarian egg diameter; uterine width; embryo number and nidamental gland width.

2.1.1 Trawl Surveys.

The surveys were carried out using the *Mary M* according to the sampling protocol developed by the Marine Institute for deepwater surveys (Clarke *et al.*, 1999; Connolly and Kelly, 1994; Kelly *et al.*, 1997b; Kelly *et al.*, 1998). The fishing gear used was a commercial Bobbin Trawl (Gundry's Ltd.©). Appendix II contains details of trawling gear. Trawling was carried out within fixed areas of the Rockall Trough and Porcupine Bank (Fig. 2.1). During the first and second surveys fishing took place in all 8 areas, over the depth ranges given in Table 2.1. The third survey only covered areas 1 to 5. Trawling in the third survey was carried out in 200 m depth strata from 500 to 1,300 m. It was not always possible to carry out tows in all of these strata in each area. Suitable fishing positions were not available for all depths. Bottom type and weather conditions prevented trawling of certain areas.

After hauling, the catch was lowered to the stern fish deck where the commercial species were removed by the crew for gutting and washing. All *Centrophorus squamosus* and *Centroscymnus coelolepis* were removed for sampling. The carcasses were then washed and stored in the hold along with the rest of the landings. The crews regarded *Deania calcea* as non-commercial and samples of this species were taken from the pond before they were discarded. During the 1995 and 1996 trawl surveys an attempt was made to sample all three species of the sharks. However, time was a limiting factor between hauls and this was not always possible. During the 1995 surveys, sampling of sharks was not considered a priority, however, spines were taken and stored dry in Sterilin® tubes. These were subsequently transferred to 70 % alcohol at the laboratory. Length frequency measurements were taken where possible. In the case of the 1997 trawl survey all specimens of the three species caught were sampled for length, weight, sex and stage of maturity. In cases where it was not possible to obtain length, weight, sex and maturity measurements from the sharks, length frequency information by sex was taken.

2.1.2 Long-line Surveys

Three long-line surveys were undertaken to provide samples for this study. The first took place in November and December of 1995, using the chartered long-liner *Sea Sparkle* of Greencastle, Co. Donegal. This boat had recently been re-fitted as a long-liner. The second long-line survey (August 1997) employed the Norwegian vessel *Skarheim*, a dedicated liner. The third also used a dedicated auto-liner, the *Loran* of Norway and took place in November/December 1999. These surveys are detailed in several publications (Connolly and Kelly, 1996; Connolly and Kelly, 1997; Connolly *et al.*, 1999 and Clarke, 1999b). The specifications of the long-line gear are detailed in Appendix II.

For the 1997 and 1999 survey size 7 and 13 hooks were deployed. The small (7) hooks were used to target small sharks, which had not been caught on any previous survey. All commercial shark species, *Centrophorus squamosus* and *Centroscymnus coelolepis* were removed from the fish-pond first and sampled. *Deania calcea* samples were taken from the catch that was being discarded. During the 1995 survey sharks were measured, weighed and sampled where possible. During the 1997 and 1999 surveys all sharks of the 3 species under review were measured and weighed.

2.1.3 Port Sampling

Four separate sampling visits were made to Lochinver in Scotland, where most of the French trawlers targeting deepwater sharks land their catches from the Rockall Trough. Samples were taken of *Centrophorus squamosus* and *Centroscymnus coelolepis* as these were the only species being landed. One sample was taken from each of the four quarters (seasons) over two years; March 1997, July 1997, December 1997 and June 1998. It was not possible to secure a 2nd quarter sample during 1997. During the first port sampling trip length, weight sex and maturity of specimens was taken. Dorsal spines, vertebral centra and gonads from both sexes were frozen at –20^{0}C for one month and then transferred to 70 % alcohol (spines and centra) and 4 % buffered formaldehyde or 4 % saline formaldehyde (gonads). For the subsequent sampling trips, length, weight, sex and maturity information were collected. Spines

were collected but vertebral centra were not, as their removal adversely effected the filleting of the sharks. Gonads that were stored in 4 % saline formaldehyde in 12 oz jars and transferred to 4% buffered formaldehyde on returning to the laboratory. Spines were stored in 70% alcohol. In some cases saline 4% formalin was used, on these occasions the material was transferred to 4 % buffered formalin on returning to the laboratory.

2.1.4 Data storage and data management

All data collected during the survey were imputed onto a Microsoft Access© relational database. This database was designed as part of the international project PL 95 O655 (EC FAIR, 1999) to store all deepwater survey-related data collected by the Marine Institute. A detailed manual (Kelly, 1997) provides details of the data formats, tables, queries and calculations used. The database contains data on each survey, the positions and depths fished. It also contains information on trawl and long-line configurations, haul composition, species information, catch data, catch per unit effort data and discard information. The database uses a data exchange format agreed by all the partners in the EU FAIR PL 95 0655 programme (Kelly, 1997). Specific information for each individual shark sampled and length frequency information were stored on Microsoft Excel© worksheets. The accuracy of the data was ensured by checking each individual entry against the raw data record sheets. A false data set was used to test the quality and accuracy of the outputs from the deepwater database.

2.1.5 Catch per Unit Effort

During the trawl surveys the total duration of fishing was recorded for each haul. Total duration was timed from when the gear settled on the ground until hauling commenced. Catch per unit effort (CPUE) was computed using routines in the Access database (section 2.1.4). In the case of trawl surveys CPUE for each haul was calculated as kg per hour of trawling;

$CPUE_{trawl}$ = kg species caught / no. hours fished

During long-line surveys the number of magazines of hooks shot at each station was recorded. For long-line surveys CPUE for each station was calculated as kg per 1,000 hooks.

$CPUE_{long\text{-}line}$ = kg species caught / number of hooks / 1,000

Values of CPUE were plotted on bathymetric maps of the Rockall Trough and Porcupine Bank areas using Surfer© (Golden Software, 1995) for each survey and species.

2.1.6 Discard rate

Discards are defined as that part of the catch returned to the sea as a result of economic, legal or aesthetic considerations (Alverson *et al.*, 1994). Discarding of fish at sea has been recognised by fisheries scientists as an inherent problem in the management of fisheries worldwide. Of the 3 species under study, *Deania calcea* is the only species discarded. In some instances the livers are retained by some vessels but the carcass is discarded in all cases.

Discarding of sharks during the 1995 and 1996 surveys was estimated using the protocols outlined by Connolly and Kelly (1996), which were based on those used by ICES Working Groups for the Assessment of Northern Shelf Stocks (Anon., 1998). Discards were placed in baskets and the number of baskets recorded. A representative

sample was taken, weighed and separated according to species. For each species length (total, pre-anus or pre-anal fin, where appropriate) and weight was recorded for the entire sample. Where weights were not taken, length-weight regressions (Coull *et al.*, 1989) were used to estimate weight. For each haul the number of boxes of commercial fish, termed landings, was recorded on the tally-sheet used by the crew. From the information on the commercial landings and the discards, the total catch was calculated thus;

Total Catch = Discards + Landings

The sample was raised to the total catch using a raising factor (R.F.);

R.F. = Dt / Ds

Where;

Dt = Total weight discarded

Ds = Weight of discards sampled.

This raising factor was used in each case to estimate the species-specific weight composition of the haul, based on the sample obtained. During the 1997 and 1999 surveys all the shark species under study were considered a priority for sampling and estimates of discard rates were not required.

The rate of discarding per tonne of target species landed was calculated in each case for trawl surveys. There is some difficulty in choosing the target species for this purpose, however *Centrophorus squamosus* and *Centroscymnus coelolepis* were chosen as they are landed collectively as "siki" and trawlers in this area only land these two deepwater sharks. Furthermore, accurate landings statistics are available for the "siki" category for French vessels. Plate 2.4 shows landings of "siki". These species was chosen for the purposes of calculating discard rates from these surveys. During the trawl surveys all species of sharks were routinely discarded. This was because of marketing problems. In areas 1 to 5 (Fig. 2.1) discard rates for trawl surveys were calculated as kg per tonne of "siki" in the landings for that haul. In areas

1 – 8 (Fig. 2.1) discard rates were also calculated as a percentage of the total catch for each haul. In the case of the long-line surveys discarding was calculated as a percentage of the total catch for each haul.

In order to estimate the total weight of *Deania calceus* discarded by trawlers official landings data as reported to ICES by France and Scotland in 1996 was used. Since these landings data are based on gutted weights a factor was required to estimate round weight from gutted weight. This conversion factor was calculated using the Regression routine in SPSS *v* 9.1 (SPSS, 1999). The numbers of *Deania calceus* discarded from trawlers in 1996 were estimated based on the weights of length frequency samples. The weight of individual specimens was estimated as 2.612 kg. Total numbers were calculated using this figure and the total weights discarded.

2.1.7 Length Frequency Distributions

Length frequency (measured only) information was collected for 1,813 *Centroscymnus coelolepis*, 2.341 *Centrophorus squamosus* and 5,672 *Deania calceus.* Length frequency distributions, by sex, for the 3 species of sharks were pooled by gear type (survey-trawl, long-line, French commercial trawl). Length frequency (5cm interval) distributions were calculated for 100 m depth strata for each species. The Kolmogorov-Smirnov (K.S.) Two Sample Test as used by Sokal and Rohlf (1995) to test for significant differences between length frequencies of two populations of silver salmon, was used in this study to test for significant differences between sexes and gear types for these distributions.

2.1.8 Sex Ratios

The sex ratio (males to females) was calculated for each depth interval for the 3 species. The Chi-squared test (Zar, 1996) was used to examine the differences between observed sex ratios and the expected ratio of equal numbers of each sex.

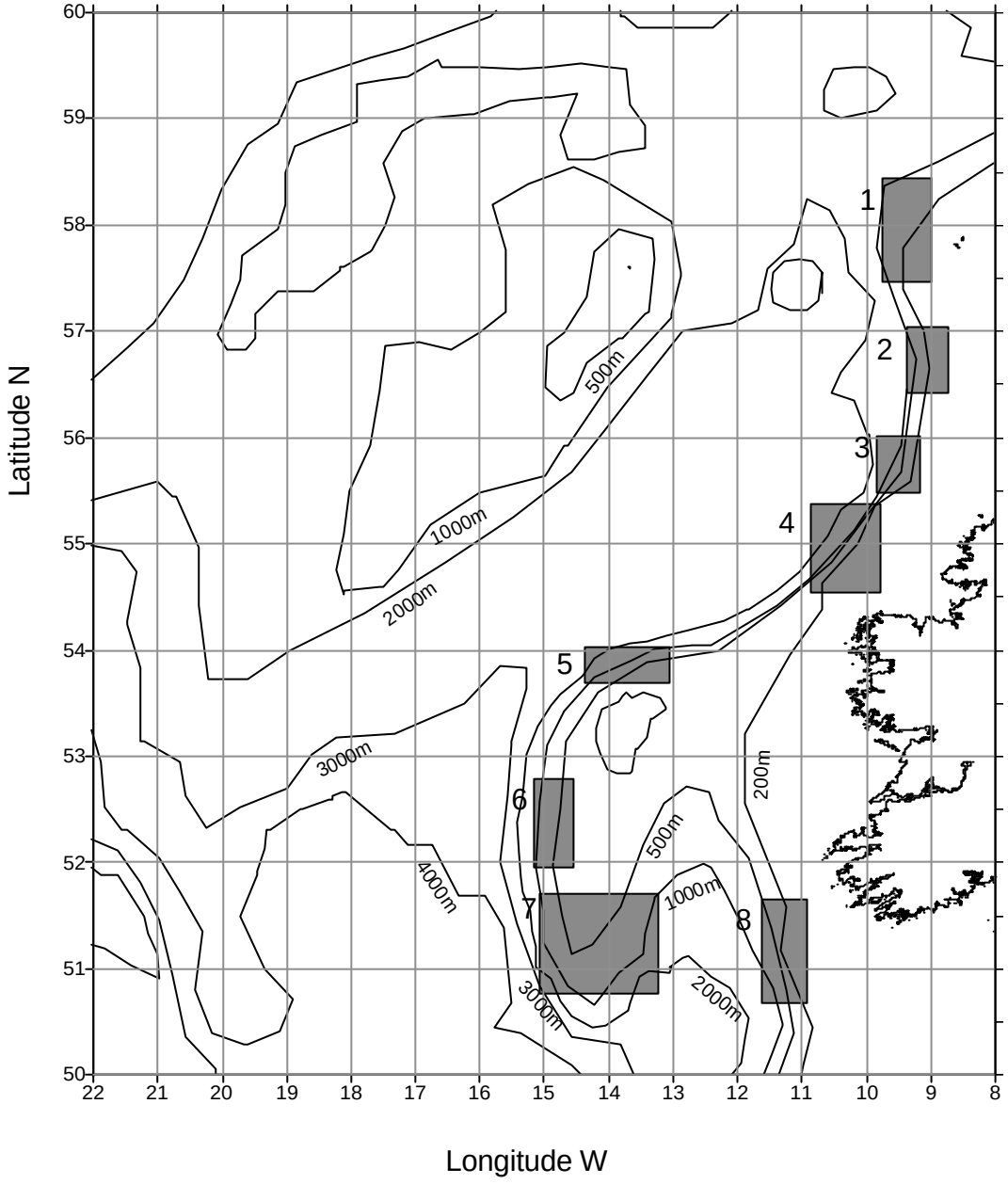


Fig. 2.1. The 8 areas where stations were completed as part of Marine Institute Deepwater survey Programme.

2.2 Age Estimation Procedures

Age estimation was attempted using both the dorsal fin spines and vertebral centra. Whole and sectioned (500 µm section using Isomet® low speed saw with diamond blade) vertebral centra were stained using crystal violet (Johnson, 1979), alizarin red (La Marca, 1966) and silver nitrate (Stevens, 1975). Sectioning of the centra was completed in the longitudinal plane along the supporting struts or intermedialia, as carried out by Walker *et al.* (1995). Whole centra were viewed with reflected and transmitted light using a Wild Heerbrugge© microscope (6 - 40 x magnification), while sections were viewed by means of a Leica Biomed© microscope (40 – 400 x magnification) and transmitted light. The centra did not display any obvious banding patterns and were considered useful for obtaining age readings. Dorsal fin spines were used exclusively for estimation of age. Histological observations were made on both sets of organs. The terminology used for describing the dorsal spines is given in Table 2.4 and illustrated in Plate 2.5 and Fig. 2.2.

2.2.1 Measurement of spines

The base diameter (Plate 2.5) of spines of *Centrophorus squamosus* and *D. calcea* was measured using a dial callipers correct to 0.1mm. Spine base diameter (SBD) was expressed as an allometric function of body length (TL) as applied by Collins (1994) to length of statoliths of squid. The relationship between spine base diameter (SBD) and total length (TL) was expressed as:

$$\mathbf{SBD = a * TL^{b}}$$

Where

a = intercept of the function

b = coefficient of regression

The regressions of SBD (mm) on TL (cm) for each dorsal fin spine were compared statistically by means of ANCOVA (Sokal and Rohlf, 1995) using the General Linear Model procedure in SPSS (1998). All data were tested for normality by means of the normal probability plot routine (Data Descriptions, 1996) and for homogeneity of

variances using Levene's statistic (Snedecor and Cochran, 1980) in SPSS *v*. 9 (SPSS, 1998). In the case of female *Centrophorus squamosus*, spine base diameter and TL data there was evidence of heterogeneous error variances ($p < 0.05$) so ANCOVA was not developed.

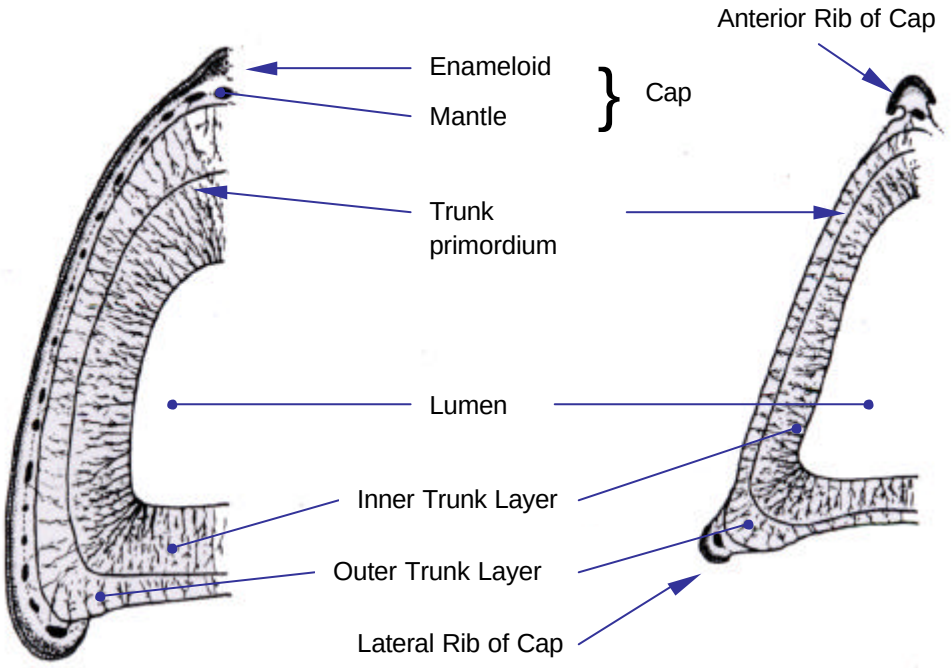


Fig. 2.2. Diagrammatic representation of internal finspine structure of *Heterodontus* (left) and of, *Etmopterus* (right) showing important features. Redrawn from Maisey (1979).

Table 2.4 Glossary of terms used in describing the dorsal fin-spine of squalid sharks together with the source references.

Term	Definition	Reference
Trunk	The main body of the finspine, deeply inserted in body	Maisey, 1979
Cap	Enamel and associated structures overlying the trunk, includes mantle	Maisey, 1979
Inner Trunk Layer	Inner concentric zone of dentine	Maisey, 1979
Outer Trunk Layer	Outer concentric zone of dentine	Maisey, 1979
Mantle	Dentinous zone of the cap	Maisey, 1979
Lumen	Central cavity	Maisey, 1979
Trunk Primordium	Thin mineralised layer separating two dentine zones	Maisey, 1979
Discontinuity	An irregular band of the inner dentine observed in distal sections	Guallart Furio, 1998
Band	Used to describe marks or rings	Wilson *et al.* 1983
Annulus	A concentric mark either a ridge, valley, translucent or opaque Does not inherently imply annual mark but is taken to mean this	Wilson *et al.* 1983
Check	An abrupt discontinuity in a ring or band	Wilson *et al.* 1983
Growth Increment	Material that exhibits a repetitive lamellar structure corresponding to a unit passage of time	Wilson *et al.* 1983
Opaque	A zone that inhibits the passage of light Transmitted light: dark Reflected light: bright	Wilson *et al.* 1983
Translucent	A zone that allows the passage of light Transmitted light: bright Reflected light: dark	Wilson *et al.* 1983
Validation	Proving that an age estimation technique is accurate Accuracy can be proven or estimated	Wilson *et al.* 1983
Verification	Determining the precision of an age estimation technique Precision relates to the reproducibility of the estimate	Wilson *et al.* 1983

2.2.2 Treatment of Spines of *Centrophorus squamosus*

Dermal denticles and connective tissue were removed from the spines by placing them in a 4% hypochlorite solution for up to 28 hours. Spines were then washed in running tap water for up to 4 hours and air-dried. Marks on the enamel layer of the spine were examined and counted using a Leica Zoom 2000 © stereomicroscope with 10 x objective and reflected light. Spines were sectioned using a Buehler © low speed jewellers saw with diamond blade at speed 1 to 2 (local setting). Sections of 500 µm were made at intervals of 2000 µm along the length of the external spine in order to make comparative counts. Spine sections were read using a Leica Biomed © microscope using 40 x magnification and transmitted light. Maximum band count was found in those sections taken immediately proximal to the constriction of the central cavity. Sections were placed in xylene to remove dirt and grit and allowed to dry overnight in a fume cupboard before mounting on glass slides using polyester resin (resin C).

The precision of the age estimates between 1st and 2nd dorsal spines were compared within sexes using the coefficient variation (CV) (Campana *et al.*, 1995).

2.2.3 Treatment of Spines of *Centroscymnus coelolepis*

Dermal denticles and connective tissue were removed from the spines in the manner described in 2.2.2 above. Spines were placed in rectangular moulds of 7 cm x 15 cm containing a 1 mm layer of unsaturated polymer resin hardened with methyl ethyl ketone peroxide in phthalate plasticiser. Spines were oriented such that the constriction of the lumen was positioned along the midline of the mould. The moulds were then filled to the top with this resin mixture. The resin blocks were removed from the moulds after 36 hours and allowed to dry for 2 weeks. Blocks were sectioned on the Isomet® low speed saw at a speed of 1 to 2 (500 µm), following a protocol followed by the Marine Institute for sectioning gadoid otoliths. Sectioned blocks were adhered to glass slides with polyester resin (resin C). Sections were examined using Leica Zoom 2000© stereo-microscope with x 10 magnification. Spine sections were read using a Leica Biomed© microscope using x 40 magnification and transmitted

light. While a series of translucent and opaque bands were visible in cross-sections, there was not sufficient clarity, and counts of bands were not possible.

2.2.4 Treatment of Spines of *Deania calceus*

Dermal denticles and connective tissue were removed from spines in the manner described in 2.2.2. Spines were then washed in running tap water for up to 4 hours and air-dried. Marks on the enamel layer of the spine were examined and counted using a Leica Zoom 2000© stereo-microscope with x 10 magnification and transmitted light. Spines were sectioned using a Buehler© low speed jewellers saw with diamond blade. Sections were taken as described in 2.2.2. Maximum band count was found in those sections immediately proximal to the constriction of the central cavity. Sections were placed in xylene to remove dirt and grit and allowed to dry overnight in the fume cupboard before mounting on glass slides using resin C. Spine sections were read using a Wild Heerbrugge© microscope using x 50 magnification and transmitted light.

The precision of the age estimates between 1st and 2nd dorsal spines were compared within sexes using the average of the coefficient of variation (CV) (Campana *et al.*, 1995). The coefficient of variation (CV) expresses the standard deviation as a percentage of the mean of paired age estimates

2.2.5 Readability of spine cross-sections

Spines were interpreted and scored according to a modification of the classification of Elder (1976) as "easy, readable, readable with difficulty or unreadable" according to the ease of interpretation of band counts. The results of these readability scores were presented as percentages of the total number of spines. To examine differences in age estimates from each spine from the same fish the difference between the 1st spine and that of the 2nd (1st spine estimate minus 2nd spine estimate) was plotted as a function of age estimate (Campana *et al.*, 1995).

2.2.6 Growth Curves

Counts from the inner dentine layer were used to construct empirical growth curves for males and females of *Centrophorus squamosus* and *Deania calceus* using the mean length for each age group. A one-way analysis of variance was used to test the null hypothesis, that there was no significant difference in mean length at age between adjacent age groups ($p < 0.05$) following the procedure of Connolly (1986).

It was not possible to apply the von Bertalanffy, Gompertz or Logistic growth models to the age estimate data due to lack of smaller (and younger) individuals of *Centrophorus squamosus* from the study area. For *Deania calceus* the length at estimated age from the current study was combined with data on this species off Portugal, published in graphical form by Machado and Figueiredo (2000). The von Bertalanffy growth model was fitted to the combined data sets for males and females. This model describes growth in length and weight for many fish adequately (Ricker, 1975).

The von Bertalanffy growth function can be described as;

$$L_t = L_\infty \left(1 - \exp^{-K(t - t_0)} \right)$$

Where;

L_t = length at time t

L_∞ = asymptotic length, or mean maximum length

K = K is a rate constant with units of reciprocal time (years $^{-1}$).

t_0 = age of the fish at theoretical zero length

The von Bertalanffy growth function was fitted to length at estimated age for males and females separately by means of the Levenberg-Marquardt algorithm using the non-linear regression routine in SPSS *v*. 9.1 (SPSS, 1999).

2.3 Reproduction

2.3.1 Maturity

Maturity was assessed during on-board and port sampling by means of the maturity scale devised for use in the EC FAIR deepwater research programme (Stehmann, 1998) see Appendix III. There was a difficulty in differentiating between stages 3 and 4 for males. Therefore the scale for males was altered by combining stages 3 and 4. During sampling episodes 989 specimens of *Centrophorus squamosus*, 1,034 of *Centroscymnus coelolepis* and 1,360 of *Deania calcea* were classified according to this maturity scale.

The proportion of mature male and female fish per 1cm total length increment was calculated for all samples combined for each species. Mature fish comprised all specimens of all maturity stages except 1 and 2. Total length at 50 % maturity for each species was determined by using the Probit model where the standard deviates of the cumulative percentages are coded by the addition of 5.0 to avoid negative values for most deviates (Sokal and Rohlf, 1995). Probit analysis has been used to examine dosage-mortality plots in toxicology and was applied to maturity data of Greenland halibut by Bowering (1983). Probit analysis was carried out using SPSS (1999). Number and position of missing year classes can lead to variations in estimates of size at maturity, depending on which model is used (Trippel and Harvey, 1991). Therefore the total numbers and the numbers mature for each centimetre length class were documented.

There was some difficulty in differentiating between stage 2 (ripening) and stage 7 (post-natal) female *Centrophorus squamosus* using the maturity scale. This was because some specimens displayed characteristics of both maturity stages, having dilated uteri, the interior of which was vilified. Villi are present in the uteri of post-natal *Centroscymnus coelolepis* and have been implicated in the supply of nutrients to the embryos (Girard and DuBuit, 1999).

In order to examine the behaviour of testes and uteri throughout the maturity cycle, as classified according to Appendix IV, the width of testes and uteri, and the weight (g)

of the testes, were measured by means of a 0.1 mm dial calliper. Paired sample t-tests (Zar, 1996) were used to test for significant differences among mean left and right testis and uterus widths. The relationship between testes and uterus width (TUW) in mm and TL (cm) was expressed as an allometric function of the type:

$$\mathbf{TUW = a * TL^{b}}$$

a = intercept

b = regression coefficient

This equation was calculated by natural logarithmic transformation of variables as:

$$\mathbf{\ln T\text{-}U\ W = \ln a + b * \ln TL}$$

Homogeneity of regression coefficients among maturity stages was tested using ANCOVA (Sokal and Rohlf, 1995) using the GLM procedure (SPSS, 1998). Where ANCOVA found evidence of heterogeneity, Gabriel's approximate method (Sokal and Rohlf, 1995) was used to test for significant differences ($p < 0.05$) among coefficients for each maturity stage. ANCOVA and Gabriel's approximate method has been used to analyse otolith weight-length regressions for Baltic Sea cod (Cardinale *et al.*, (2000). Where there was evidence of homogeneity, ANCOVA was developed to test for heterogeneity among regression intercepts. Where intercepts were heterogeneous ($p < 0.05$) Gabriel's approximate method was employed to test for significant differences among intercepts (Sokal and Rohlf, 1995). All data were tested for normality by using the normal probability plot routine (Data Descriptions, 1996) and for homogeneity of variances using Levene's statistic (Snedecor and Cochran, 1980) in SPSS *v*. 9 (SPSS, 1999).

While Ricker (1973 and 1975) recommends Model II regression, Model I regression was used in this study for the analysis of allometric data because of the lack of statistical tests for Model II (see Appendix IV).

2.3.2 Gonadosomatic Index

The changes in testis and ovary weight were investigated using the gonadosomatic index (G.S.I.) as used by Ellis and Shackley (1997) and calculated as;

Gonad Weight (g) / Total Weight (g)* 100

for the changes in gonad weight throughout the process of maturation.

2.3.3 Hepatosomatic Index

Hepatosomatic Index (HSI) as defined by Francis (1997) was calculated as

HSI = Liver Weight (g) / Total Weight (g) * 100

HSI was calculated for each sex maturity stage for *Centrophorus squamosus* and *Centroscymnus coelolepis*.

2.3.4 Treatment of gonads

In order to assess the reproductive maturity of the three shark species and to verify the gross maturity scale (2.3.1), histological investigations of the gonads were undertaken according to the techniques outlined by Humason (1972). Gonads were stored in 4% buffered formalin for periods, from 1 month to 3 years. Sections were taken from the mid portion of the testis and placed in tissue-cassettes. Sections were infiltrated with wax by means of a Tissue Tek® Vacuum Infiltration Processor, for infiltration protocol see Appendix V. Specimens were embedded in paraffin wax by means of a Shandon Histo-Center© embedding apparatus. Sectioning was carried out using a Leida© RM 2035 rotary microtome (blade angle of 6^0) with disposable blades at a thicknesss of 4 µm. All specimens were stained with stabilised activity 3 Haematoxylin and counter stained with alcoholic Eosin using a Shandon Veristain© 24-3 rotary stainer. See Appendix VI for protocol of staining procedure. On removal from the stainer the slides were immediately cover-slipped using a Tissue Tek ® automatic cover-slipper.

2.3.5 Interpretation of gonad slides

Slides were observed using Nikon© compound microscope, with Panasonic F10© Video camera at 4 x, 10 x and 40 x magnification. The types of spermatocytes present in each testis examined were recorded in each case. Spermatogenic stages were classified according to the descriptions of Parsons and Grier (1992).

To investigate if there was seasonality in the production of ripe spermatozoa, slides of the testes of 6 adult (stage 3) specimens were selected at random. Six slides per month for which samples were obtained were selected, for each species. Spermatocysts containing spermatozoa from each spermatogenic phase were counted using the Interactive Measurement routine in Leica Q500MC image analysis system (Leica, 1995). The frequency of occurrence of each phase of spermatogenesis in each section was used to construct a monthly frequency histogram by month showing the relative numbers of each phase. The counts were analysed using a one-way analysis of variance to test the null-hypothesis that there was no significant difference between

counts of each stage between months ($p < 0.05$). The spermatogenic phases considered were as follows:

I Spermatocysts with Spermatogonia
II Spermatocysts with Primary Spermatocytes
III Spermatocysts with Secondary Spermatocytes
IV Spermatocysts with Spermatids
V Spermatocysts with Ripe Spermatozoa
VI Evacuated spermatocysts

2.3.6 Fecundity

The number of ripe or ripening ovarian eggs, was recorded. The number of embryos in each uterus was also recorded. Ovarian and uterine fecundity was plotted as a function of total length for *Centroscymnus coelolepis*. In the case of *Centrophorus squamosus* no gravid females were recorded, hence ovarian fecundity alone was presented. Regression analysis was not performed on fecundity data because of the high variances associated with the fecundity data. This was noted by Silva and Ross (1993) for *Squalus acanthias*. Only a small number of gravid *Deania calceus* specimens were found during this study and of those only 2 contained near-term embryos.

2.4 Mortality

The instantaneous rate of total mortality (Z) of *Deania calceus* was estimated by linear regression of the natural logarithm of numbers in the catch for the 1999 long-line survey on age estimates. The absolute value of the regression coefficient of the falling limb of catch numbers at age provides an estimate of Z (Ricker, 1975). Numbers of fish in the total catch were partitioned into age groups by use of mean length at age information for each species based on 1st dorsal spines. The very oldest age groups were excluded because of larger catch numbers in some cases, indicating a decreased mortality for some of the oldest estimated age groups. These accounted for a very small percentage of total numbers and their exclusion insured that Z was

estimated across those age groups which were well represented in the catch. Survivorship (S) was calculated by the equation of Ricker (1975);

$$S = e^{-Z}$$

Where

S = Survivorship

e = Base of the natural logarithm

Z = Total Mortality Estimated from Catch Curve

Natural mortality (M) was estimated using the formula developed by Pauly (1980);

$$\ln M = -0.006 - 0.279 \ln L_{\infty} + 0.06543 \ln K + 0.4634 \ln T^0C$$

Where

K = Von Bertalanffy Growth Function rate function parameter.

L_{∞} = Asymptotic length from von Bertalanffy Growth Function.

T^0C = mean ambient Temperature in degrees Celsius, considered as 7^0C.

Natural mortality was estimated by a second method for *Centrophorus squamosus* and for comparative purposes for *Deania calceus*. This method is based on the assumption that M is the level of natural mortality required to reduce the recruited population to 1 % of its initial value (Rago *et al.*, 1998). The method of estimating M is outlined by King (1995, p 188-189) and is carried out thus.

$$M = -\ln 0.01 / \text{maximum age}$$

King (1995) states that in unexploited fish stocks the oldest individuals are often about 95 % of the species asymptotic length (L_{∞}). In the present case maximum age was considered to be the maximum estimated age determined from first dorsal spines.

Plate 2.1. M.F.V. *Mary M* docked in Lochinver, Scotland before trawl survey in September 1996.

Plate 2.2. M.F.V. *Sea Sparkle*, in Greencastle. Co. Donegal, after long-line survey in December 1995.

Plate 2.3. M.F.V. *Loran* in Cobh, Co. Cork after long-line survey in December 1999.

Plate 2.4. Deepwater sharks at auction in Concarneau, France, March 1997. Collectively *Centrophorus squamosus* and *Centroscymnus coelolepis* are marketed under the name "siki".

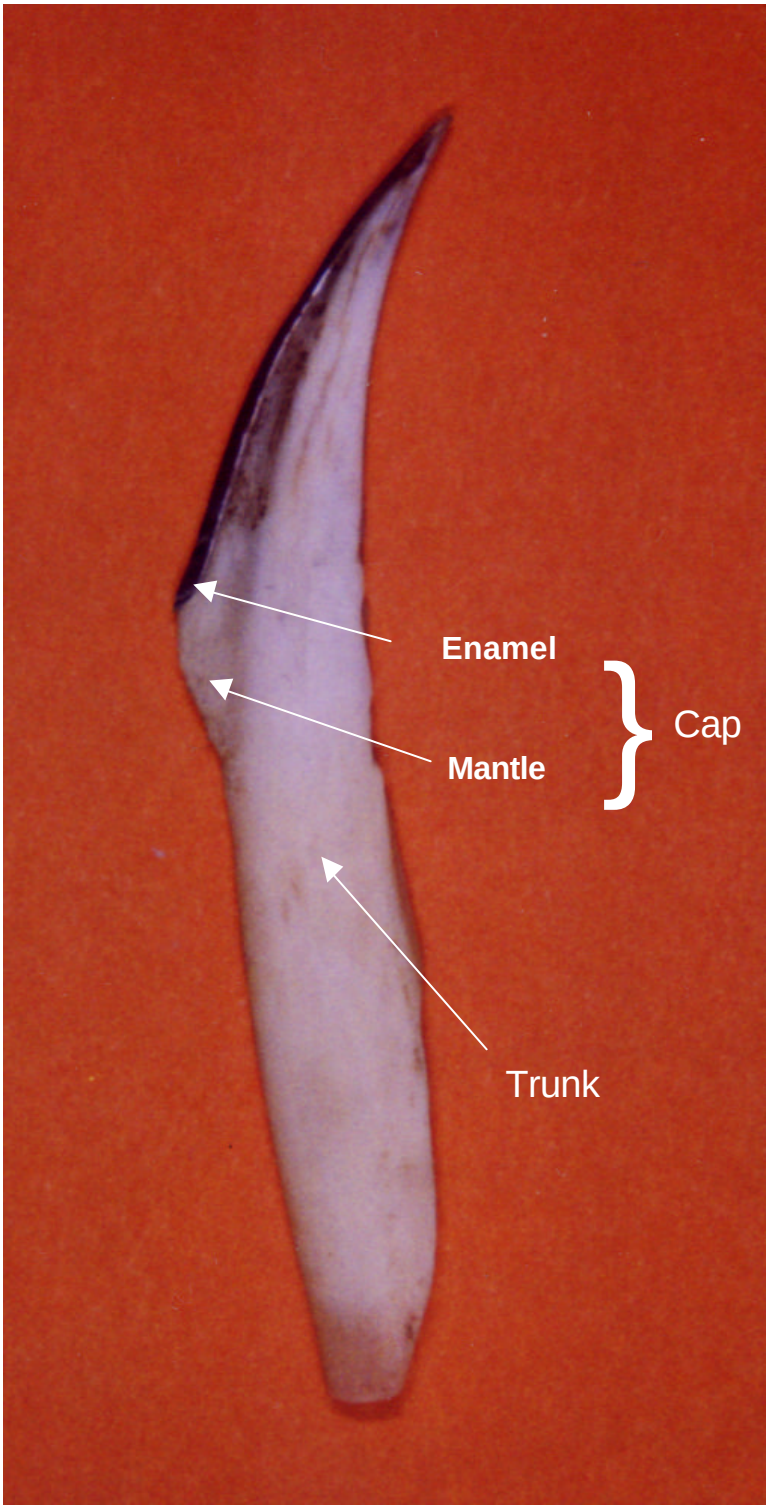


Plate 2.5. First dorsal spine of *Centrophorus squamosus* showing external features, see Table 2.4.

3 Results

3.1 Population Structure

3.1.1 Distribution of *Centroscymnus coelolepis*.

The catch per unit effort (CPUE) from trawl and long-line data are presented in Fig. 3.1 and Fig. 3.2 respectively. Highest catches were recorded in some areas of the Porcupine slopes. *Centroscymnus coelolepis* was distributed all along the continental shelf from 49^0 N to 58^0 N. High catch rates on trawl (Fig. 3.1.) were found on the southern slopes of the Rockall Trough in both 1996 and 1997. In 1997 high catch rates were recorded on the eastern slopes of the Rockall Trough. This species was widespread, though not very abundant in most areas. However, in the Porcupine Seabight catches were low.

The absolute depth range for this species was 610 m – 1,823 m. Average CPUE by 100 m depth interval is given in Fig. 3.3 for trawl and Fig 3.4 for long-line. Peak catch rates of *Centroscymnus coelolepis* from trawls lay in the 1,200 m – 1,300 m depth range, while the greatest return for long-lines came from deeper water, 1,300 m to 1,400 m. Evidently trawling did not target the entire depth range of this species in this area and that peak abundance occurs below the range of most trawlers (1,300 m).

Approximately equal numbers of each sex were present in the middle depth range (1,200 m – 1,300 m). Sex ratio significantly favoured females ($p < 0.05$) in the shallower depths and in deepest waters (Fig. 3.5). These data along with the sex ratio data for the other species are contained in Table 3.1.

Immature female specimens were absent in depths less than 1,000 m, while in depths below 1,500 m only stage 1 (immature fish) were found. They were the most numerous stage below 1,300 m. The proportions of female maturity stages by depth are displayed in Fig. 3.6 and contained in Table 3.2. There was a marked tendency for immature females to occupy deeper waters, with ripening (stage 2) and pre-ovulatory (stage 3) specimens more numerous in shallower waters. Stage 3 females were most

abundant in the middle range (1,000 m – 1,100 m) corresponding to maximum density of mature males. This indicates that mating takes place in the mid-range of depths, where abundance of *Centroscymnus coelolepis* is greatest. Noteworthy, too, was the complete absence of gravid females below 1,300 m. While there was a tendency for gravid females to locate further up the slope, post-natal sharks occurred deeper, between 1,300 and 1,400 m. Table 3.3 contains the numbers of male maturity stages by depth and the proportions of each stage are presented in Fig. 3.7.

No immature (stage 1 or 2) males were found in depths less than 1,100 m and were only a small proportion of the total in depths down to 1,300 m and there was a tendency for males to move up-slope as they mature. However, below 1,300 m they predominated over mature fish. Stage 1 immature males only predominated in depths below 1,500 m.

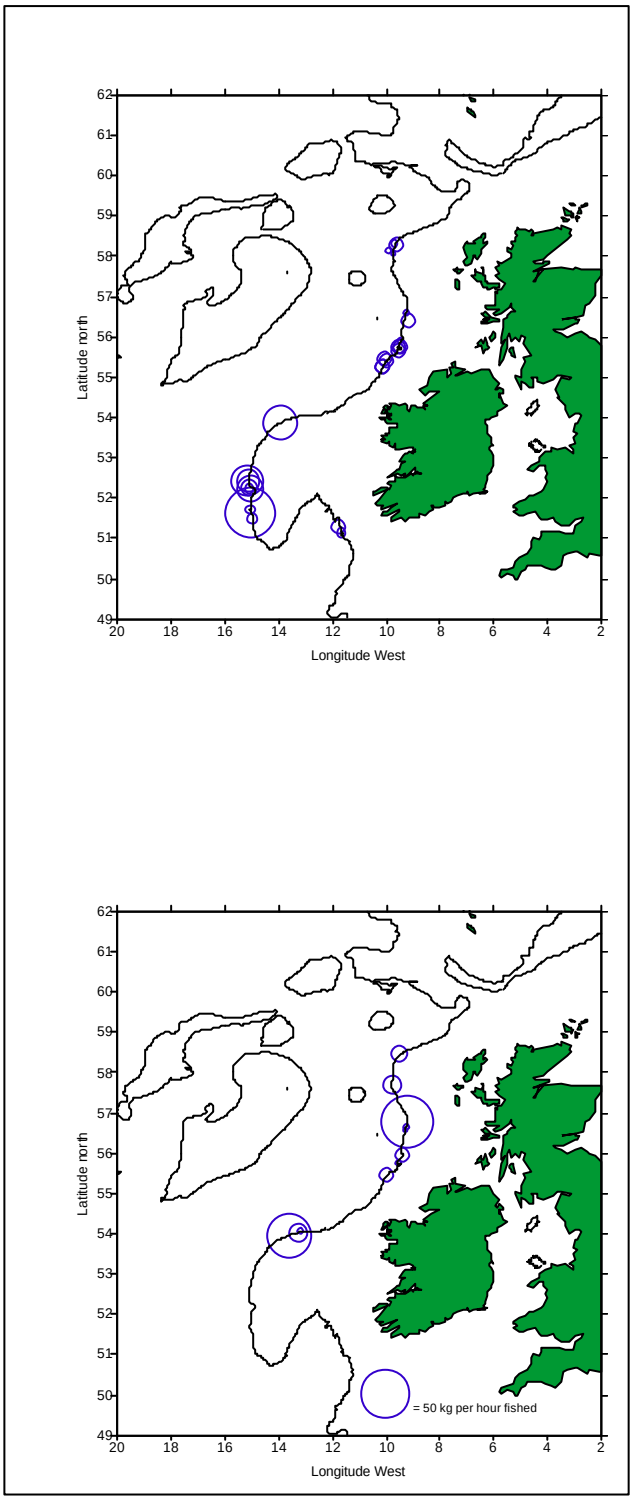


Fig.3.1. Catch per unit effort for *Centroscymnus coelolepis* in kg per hour trawled during surveys in September 1996 (top) and October – November 1997 (bottom). The 1,000 m contour is indicated.

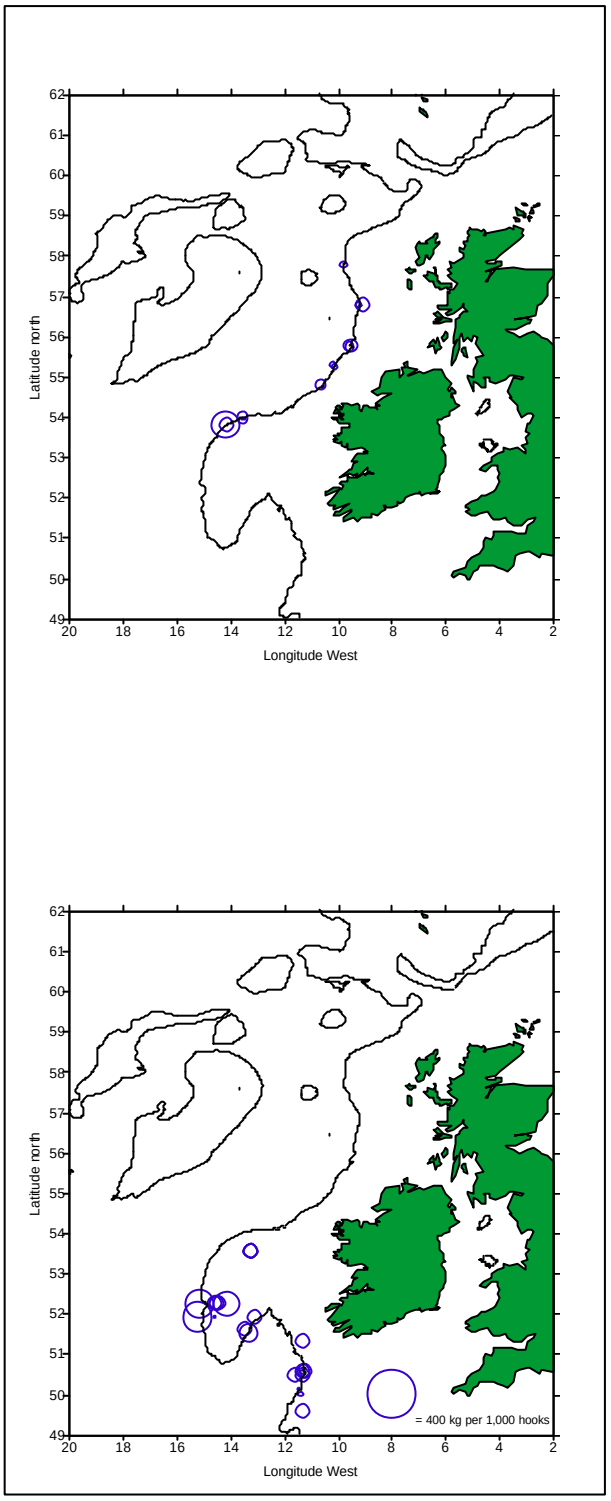


Fig.3.2. Catch per unit effort for *Centroscymnus coelolepis* in kg per 1,000 hooks during long-line surveys in August 1997 (top) and December 1999 (bottom). The 1,000 m contour is indicated.

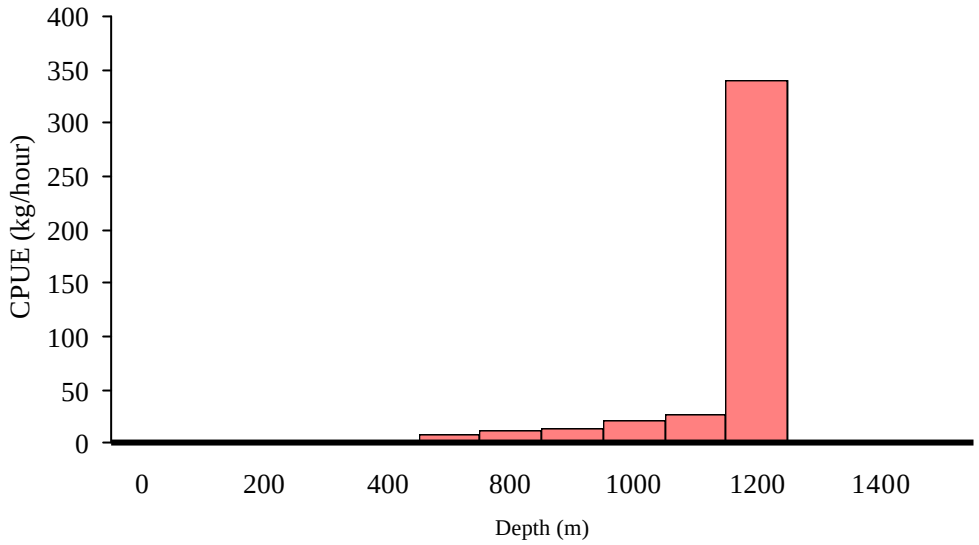


Fig. 3.3. Variation in average CPUE (kg per hour trawled) for *Centroscymnus coelolepis*, based on trawl surveys in 1996 and 1997. Each 100 m depth interval is indicated by its lower value.

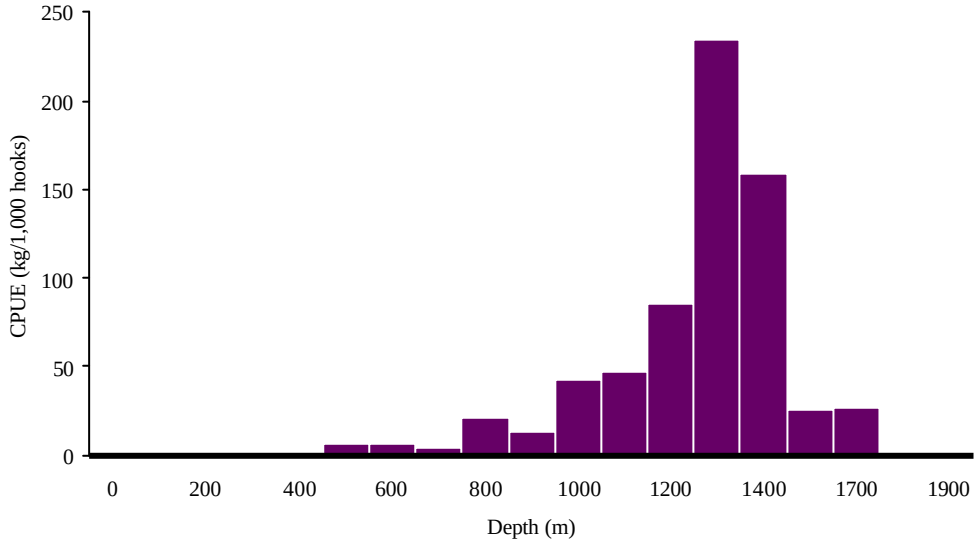


Fig. 3.4. Variation in average CPUE (kg per 1,000 hooks) for *Centroscymnus coelolepis*, based on long-line surveys in 1997 and 1999. Each 100 m depth interval is indicated by its lower value.

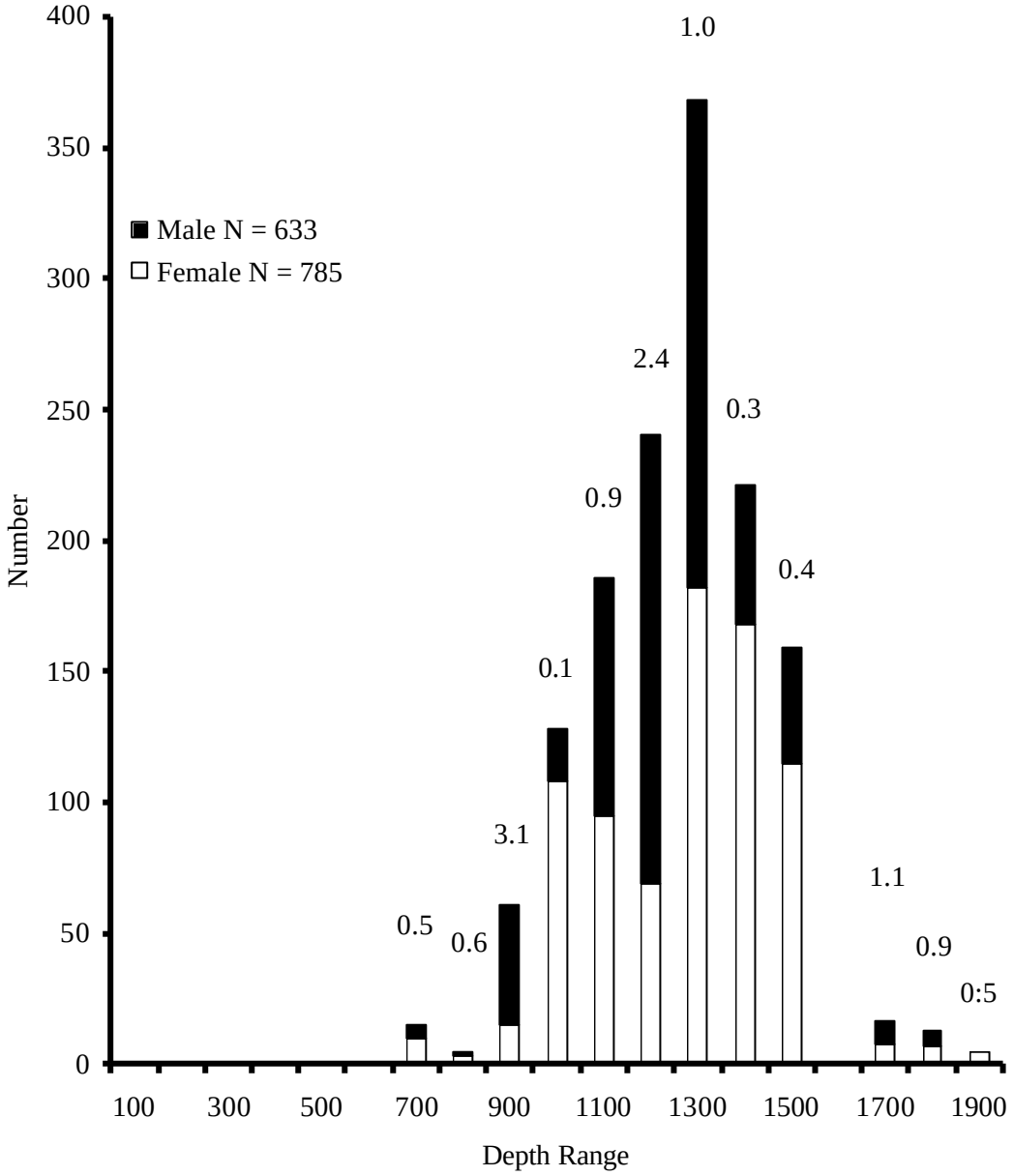


Fig. 3.5 Variation in sex ratio (males : females) with depth in intervals of 100 m for *Centroscymnus coelolepis*. Depth ranges indicated by upper value in each case.

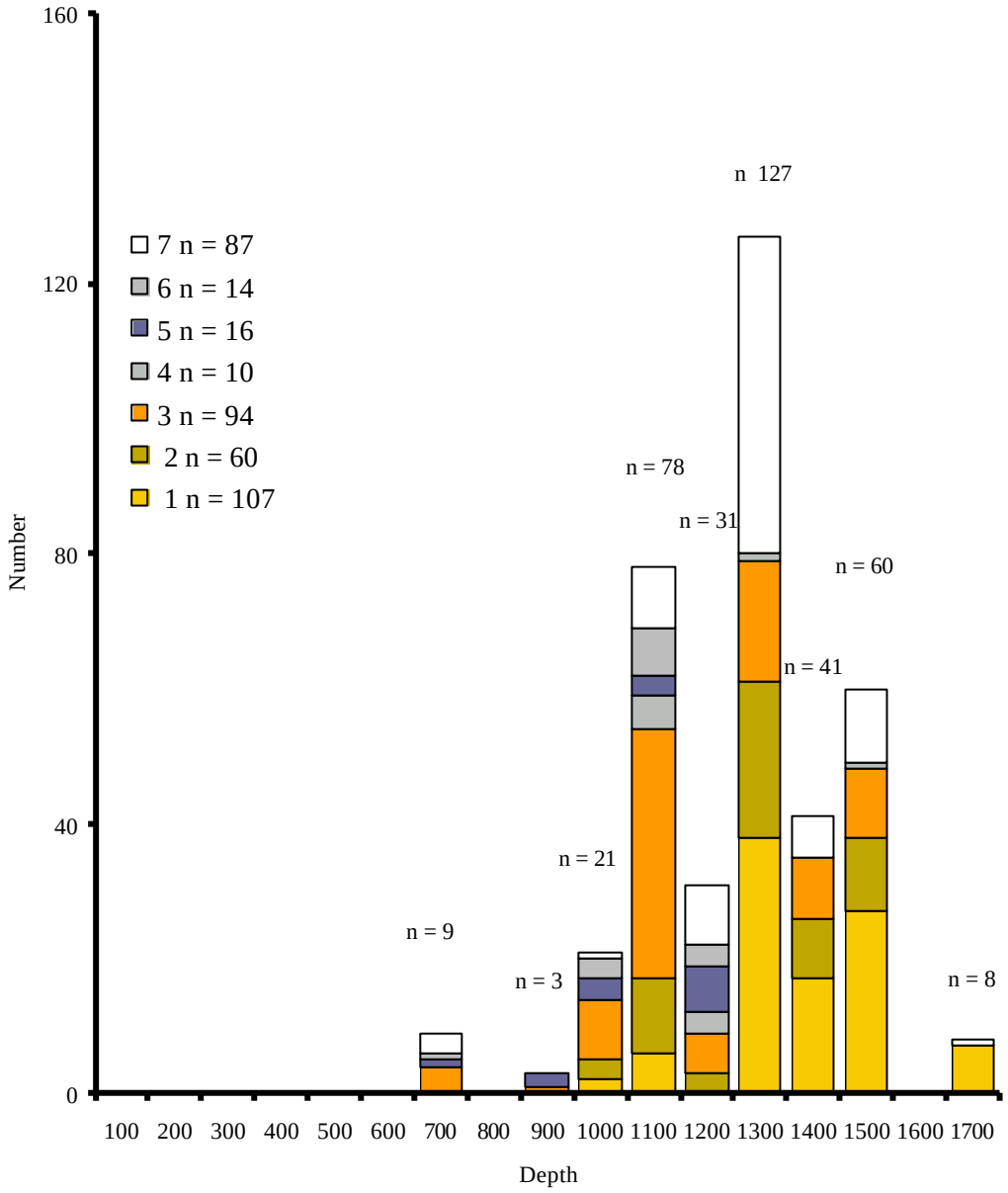


Fig. 3.6 Variation in maturity stages by depth range (100 m) for female *Centroscymnus coelolepis*. Depth interval indicated by upper value in each case.

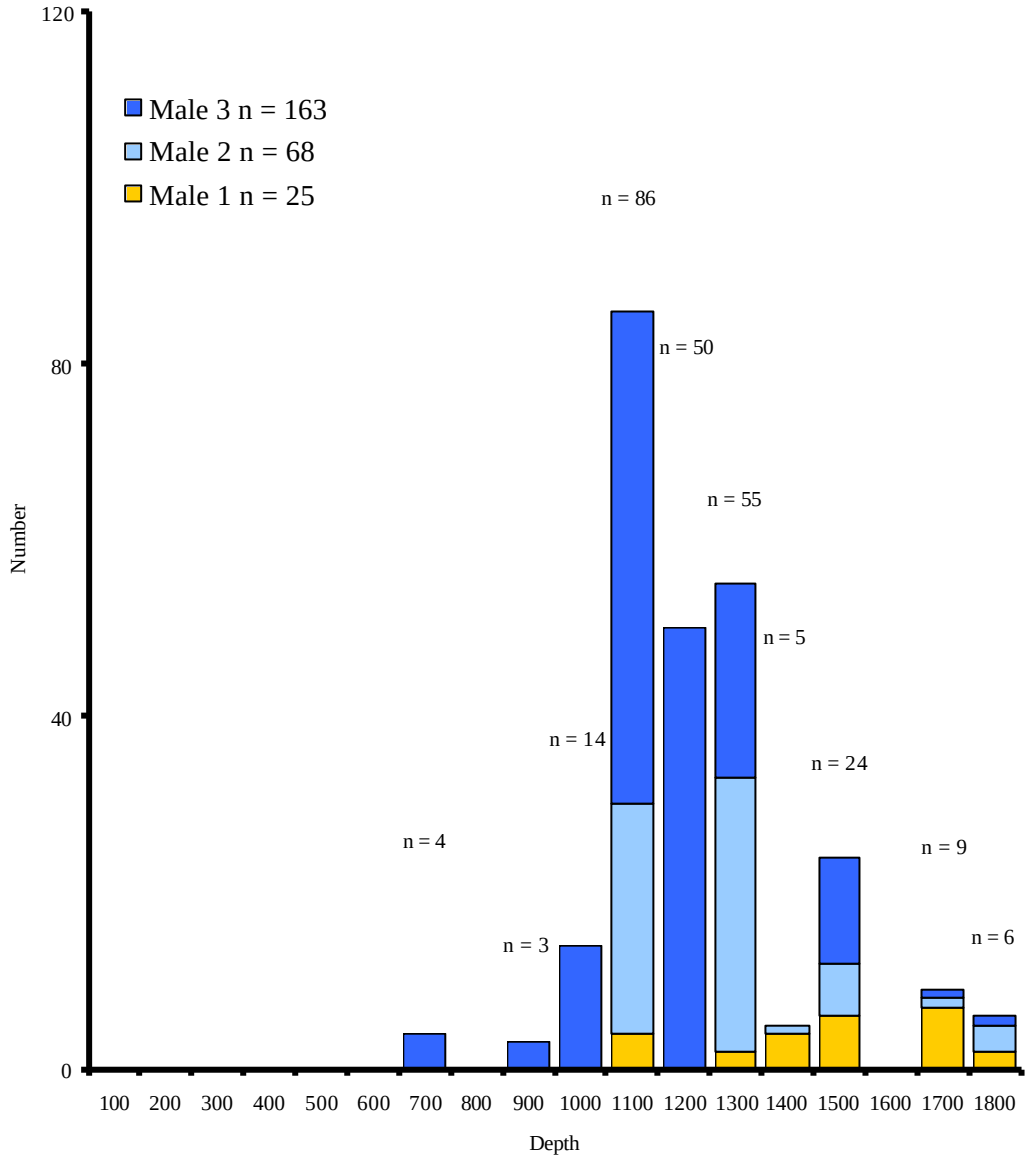


Fig. 3.7. Relative occurrence of maturity stages by depth interval in intervals of 100 m for male *Centroscymnus coelolepis*. Depth interval indicated by upper value in each case.

Table 3.1. Numbers of each sex by depth range, in 100 m intervals for *Centroscymnus coelolepis*, *Centrophorus squamosus* and *Deania calcea*. Ratio of males to females indicated for each depth and for all depths combined.

Species	Depth Range	Female	Male	Total	Ratio
Centroscymnus coelolepis	600 - 700	10	5	15	0.50
	700 - 800	3	2	5	0.67
	800 - 900	15	46	61	3.07
	900 – 1,000	108	20	128	0.19
	1,000 - 1,100	95	91	186	0.96
	1,100 - 1,200	69	171	240	2.48
	1,200 - 1,300	182	186	368	1.02
	1,300 - 1,400	168	53	221	0.32
	1,400 -1,500	115	44	159	0.38
	1,600 - 1,700	8	9	17	1.13
	1,700 - 1,800	7	6	13	0.86
	1,800 - 1,900	5	0	5	
	Total	**785**	**633**	**1418**	**0.81**
Centrophorus squamosus	500 - 600	5	7	12	1.40
	600 - 700	9	43	52	4.78
	700 - 800	115	184	299	1.60
	800 -900	21	32	53	1.52
	900 – 1,000	460	644	1104	1.40
	1,000 - 1,100	171	196	367	1.15
	1,100 - 1,200	58	45	103	0.78
	1,200 - 1,300	90	82	172	0.91
	1,300 - 1,400	26	62	88	2.38
	1,400 -1,500	10	6	16	0.60
	Total	**965**	**1301**	**2266**	**1.35**
Deania calcea	500 - 600	54	190	244	3.52
	600 - 700	242	648	890	2.68
	700 - 800	393	728	1121	1.85
	800 -900	204	317	521	1.55
	900 – 1,000	371	855	1226	2.30
	1,000 - 1,100	429	701	1130	1.63
	1,100 - 1,200	86	166	252	1.93
	1,200 - 1,300	106	155	261	1.46
	1,300 - 1,400	7	11	18	1.57
	1,400 -1,500	8	4	12	0.50
	Total	**1900**	**3775**	**5675**	**1.99**

Table 3.2. Frequency of each maturity by depth interval for female *Centroscymnus coelolepis*.

Depth	Stage 1	Stage 2	Stage 3	Stage 4	Stage 5	Stage 6	Stage 7	Total
500 -600	0	0	0	0	0	0	0	**0**
600 - 700	0	0	4	0	1	1	3	**9**
700 - 800	0	0	0	0	0	0	0	**0**
800 - 900	0	0	1	0	2	0	0	**3**
900 - 1,000	2	3	9	0	3	3	1	**21**
1,000 - 1,100	6	11	37	5	3	7	9	**78**
1,200 – 1,300	0	3	6	3	7	3	9	**31**
1,300 – 1,400	38	23	18	1	0	0	47	**127**
1,400 – 1,500	17	9	9	0	0	0	6	**41**
1,500 – 1,600	27	11	10	1	0	0	11	**60**
1,600 – 1,700	0	0	0	0	0	0	0	**0**
1,700 – 1,800	7	0	0	0	0	0	1	**8**
1,800 – 1,900	5	0	0	0	0	0	0	**5**
1,900 – 2,000	5	0	0	0	0	0	0	**5**
Total	**107**	**60**	**94**	**10**	**16**	**14**	**87**	**388**

Table 3.3. Frequency of maturity stages by depth interval for male *Centroscymnus coelolepis*.

Depth	Stage 1	Stage 2	Stage 3	Total
600 - 700	0	0	4	**4**
700 - 800	0	0	0	**0**
800 - 900	0	0	3	**3**
900 1,000	0	0	14	**14**
1,000 - 1,100	4	26	56	**86**
1,100 - 1,200	0	0	50	**50**
1,200 - 1,300	2	31	22	**55**
1,300 - 1,400	4	1	0	**5**
1,400 - 1,500	6	6	12	**24**
1,500 - 1,600	0	0	0	**0**
1,600 - 1,700	7	1	1	**9**
1,700 - 1,800	2	3	1	**6**
Total	**25**	**68**	**163**	**256**

3.1.2 Length Frequencies of *Centroscymnus coelolepis*

Length frequencies of males and females for each 100 m depth interval are presented in Fig. 3.8. The deepest portions of the species' range were occupied by small specimens, with larger females and males progressively more numerous upwards to 1,000 m. Large females were found in shallower waters. Length frequencies for the entire study combined are presented in Fig. 3.9. The length range for males was 68 cm to 109 cm and for females 71 cm to 121 cm and no smaller specimens were ever encountered. Table 3.4 contains the results of the K.S. test for comparing length frequency distributions for *Centroscymnus coelolepis*. There was a very significant ($p < 0.01$) difference in the length frequencies for each sex, with a marked sexual dimorphism and wide separation of modes evident. Trawl and long-line length frequencies for males and females are presented in Fig. 3.10. Trawl and long-line selected for significantly different length ranges of both sexes. Long-lines selected larger males not caught in trawls, though a similar effect was not found for females, where maximum length in catches from both gears were similar. However smaller females were taken on long-lines than on trawls. There was a significant difference between trawl and long-line distributions. Long-lines selected for a broader range, both smaller and bigger specimens of both sexes. French trawlers landing into Lochinver and Irish commercial bottom trawls did not produce significantly different distributions. The length frequencies for each gear type are presented in Fig. 3.11, indicating that both trawl types select for the same size range of this species. Length frequencies from trawl and long-line were significantly different ($p < 0.05$).

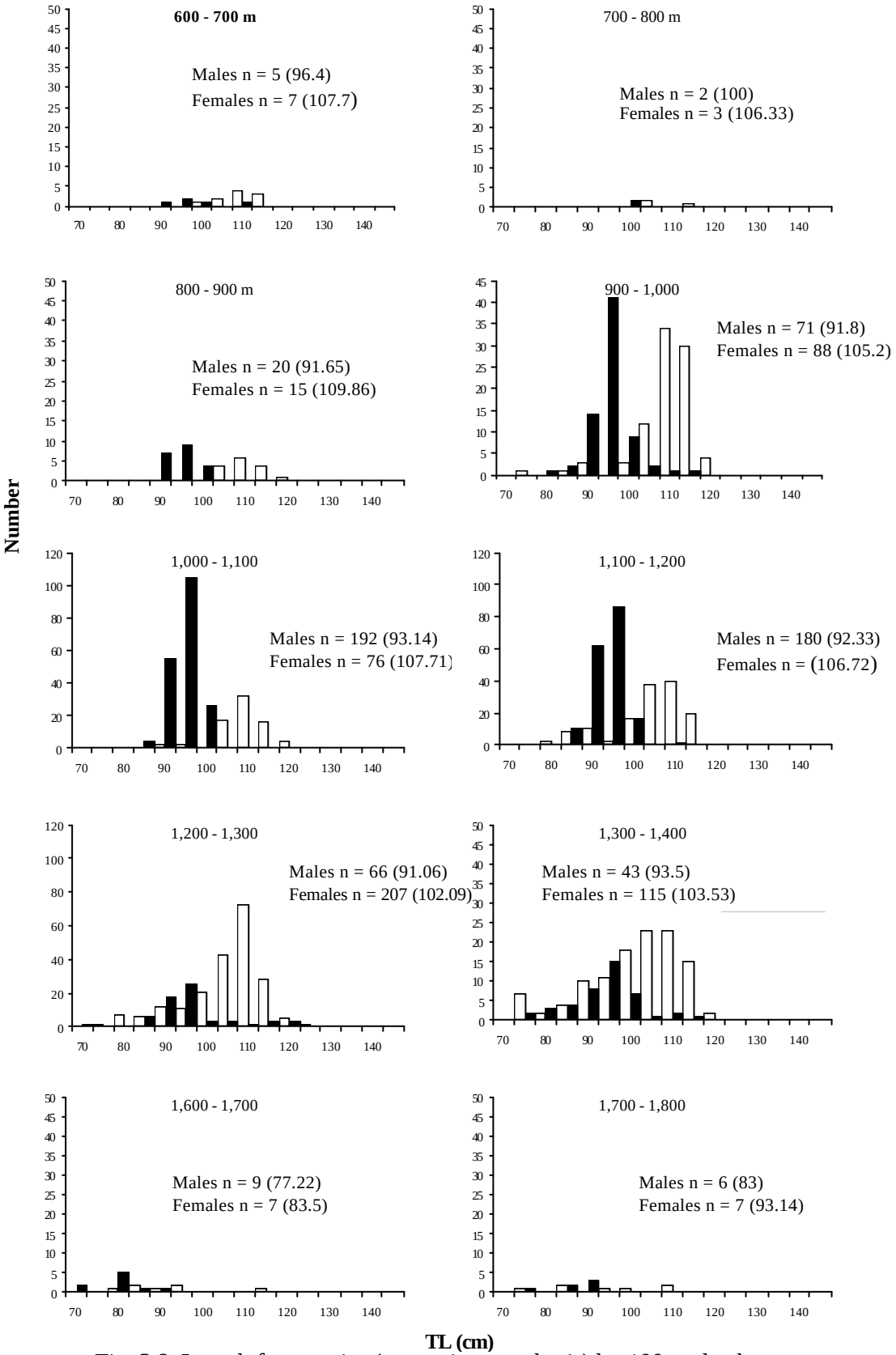


Fig. 3.8. Length frequencies (means in parenthesis) by 100 m depth interval, for *Centroscymnus coelolepis*.

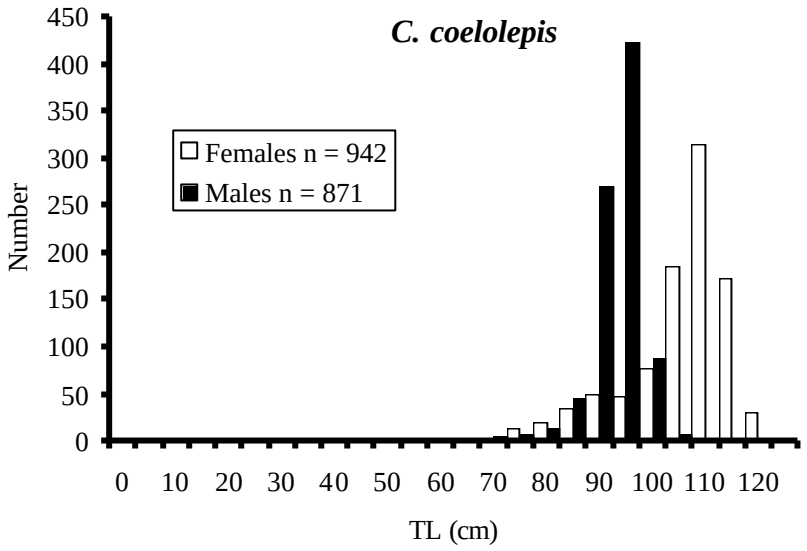


Fig. 3.9. Length frequency for *Centroscymnus coelolepis*, all samples combined.

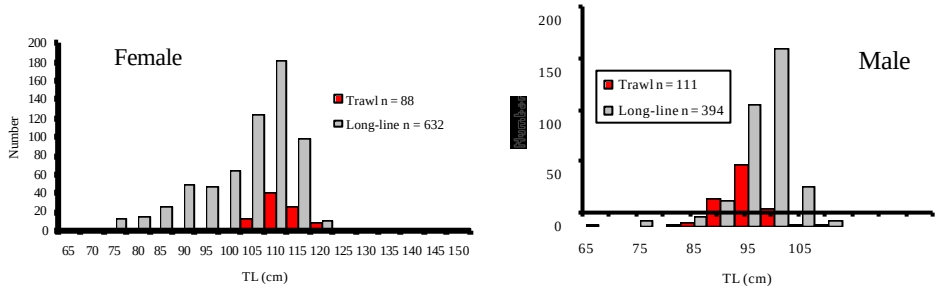


Fig. 3.10. Trawl and long-line length frequencies for female (left) and male (right) *Centroscymnus coelolepis* in 1997.

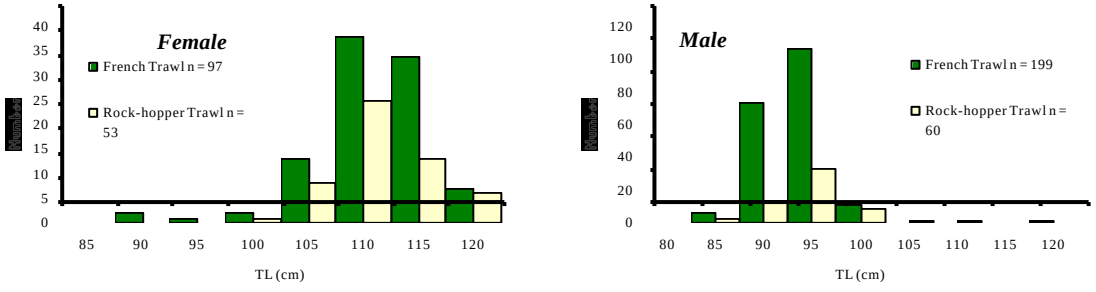


Fig. 3.11. Comparison of length frequencies of *Centroscymnus coelolepis* caught in the Rockall Trough by French commercial trawl and Irish deepwater rock-hopper trawl in 1997.

Table 3.4. Largest absolute difference and calculated critical values of the Kolmogorov-Smirnov two sample test for *Centroscymnus coelolepis*.

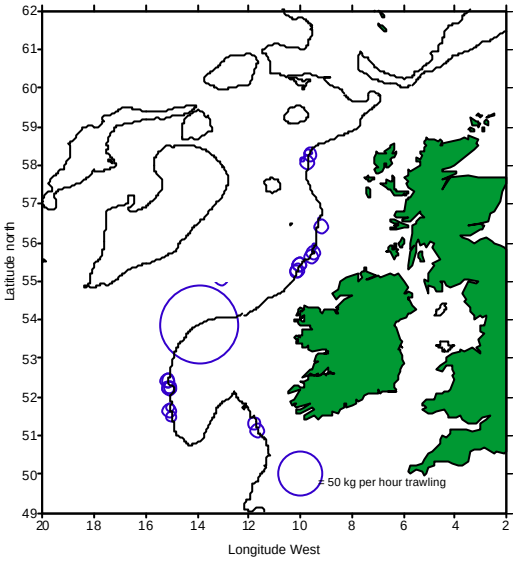
	Absolute Difference	Critical Value	Significance
Males and females all samples	0.719	0.064	S ($p < 0.05$)
Trawl and long-line caught females (1997)	0.368	0.155	S ($p < 0.05$)
Trawl and longline caught males (1997)	0.406	0.149	S ($p < 0.05$)
French and rock-hopper caught females (1997)	0.032	0.232	NS
French and rock-hopper caught males (1997)	0.118	0.2	NS

3.1.3 Distribution of *Deania calceus*

CPUE data for trawl and long-line are presented by area in Fig. 3.12 and Fig. 3.13 respectively. CPUE rates for *Deania calceus* indicate that it is most numerous in more southern locations and less so in the eastern Rockall Trough, where most trawling takes place. Gravid females were encountered only on the southern slopes of the Rockall Trough and western Porcupine. Since most trawlers operate in the Rockall Trough it probably is less susceptible to trawling pressure than *Centrophorus squamosus*. The absolute depth range for *Deania calceus* was 557 m – 1,404 m. Catch rates from long-lines covered a broader depth range. Peak catch rates were recorded in the range 400 m – 700 m. These peak catches were taken from the southern slope of the Rockall Trough. It is evident from Fig. 3.14 and Fig. 3.15 that almost the entire depth range of this species is within the range of the deepwater trawl fishery, between 300 m and 1,300 m. Trawling produced peak catches at greater depths, 900 m – 1,000 as opposed to 500 m – 800 m for long-lines.

The sex ratio indicates that males are more vulnerable to fishing than females. Sex ratios by depth interval are contained in Table 3.1 for *Deania calceus*. In all but the deepest interval from which *Deania calceus* were caught males outnumbered females. The overall sex ratio showed that males significantly out-numbered females ($p < 0.01$) by almost 2:1. Fig. 3.16 shows the proportions of males and females at each depth.

The female population was dominated by immature (stage 1) individuals, and they were particularly dominant deeper than 1,000 m (Fig. 3.17, Table 3.5). While uterine stage fish were very rare, only recorded in December 1999, they were taken in shallower waters. Mature females were most numerous in the middle range (900 m – 1,000 m). While most males in the study area were mature, and there was little evidence of depth segregation by maturity stage by maturity stage (Fig. 3.18, Table 3.6).



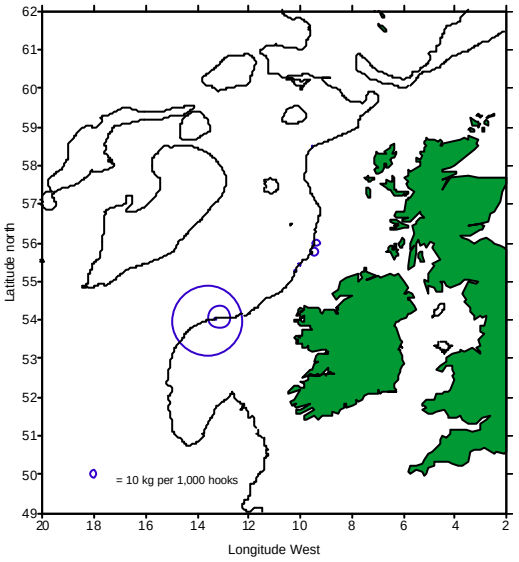
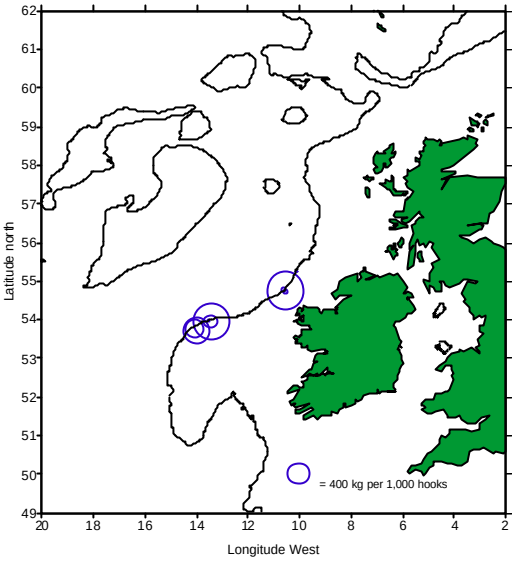


Fig.3.12. Catch per unit effort for *Deania calceus* in kg per hour of trawling on surveys in September 1996 (top) and October – November 1997 (bottom). The 1,000 m contour is indicated.



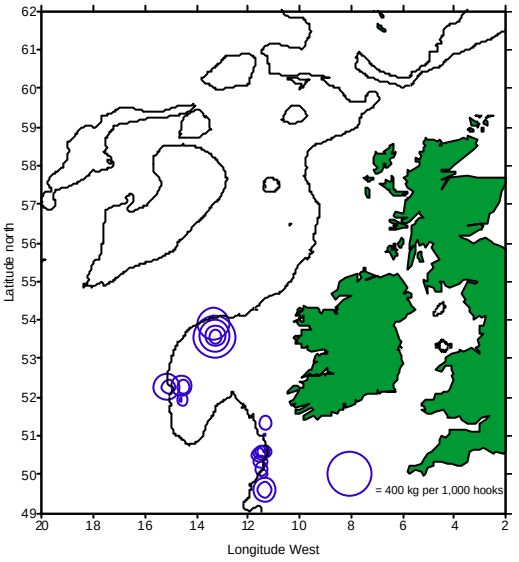


Fig. 3.13. Catch per unit effort for *Deania calceus* in kg per 1,000 hooks on long-line surveys in August 1997(top) and December 1999 (bottom). The 1,000 m contour is indicated.

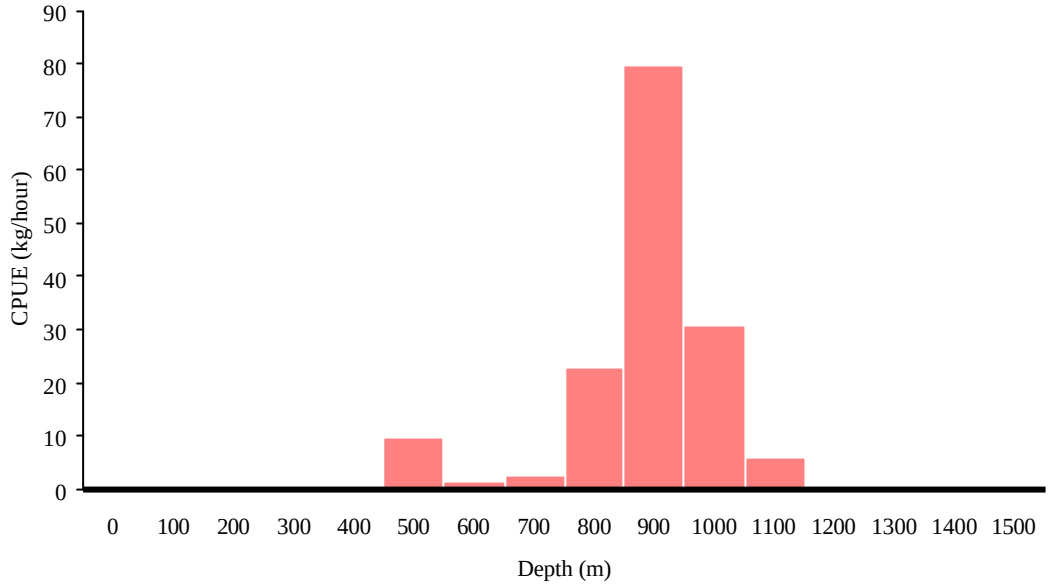


Fig. 3.14. Variation in average CPUE (kg per hour trawled) for *Deania calceus*, based on trawl surveys in 1996 and 1997. Each 100 m depth interval is indicated by its lower value.

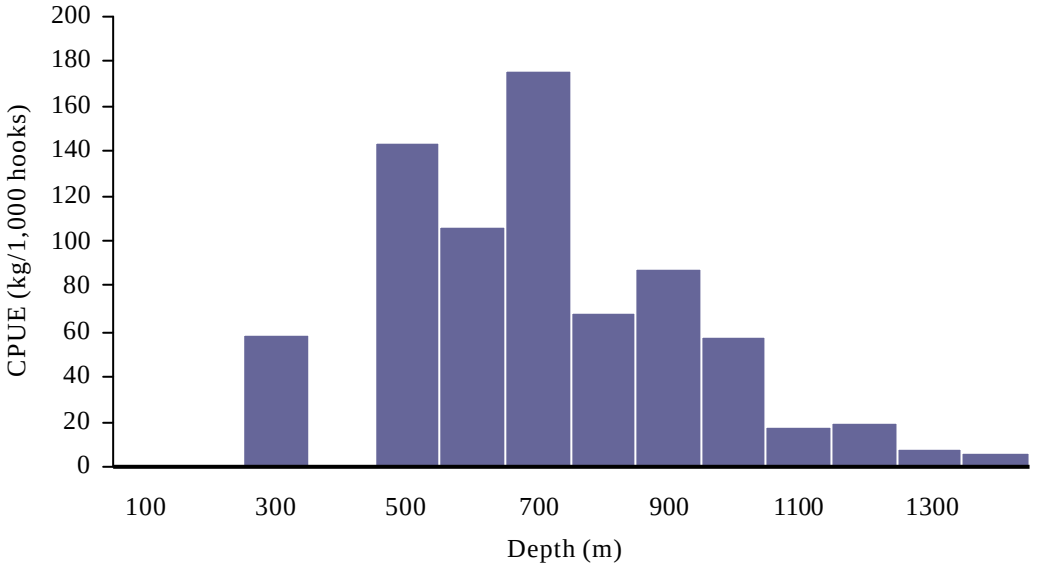


Fig. 3.15. Variation in average CPUE (kg per 1,000 hooks) for *Deania calceus*, based on long-line surveys in 1997 and 1999. Each 100 m depth interval is indicated by its lower value.

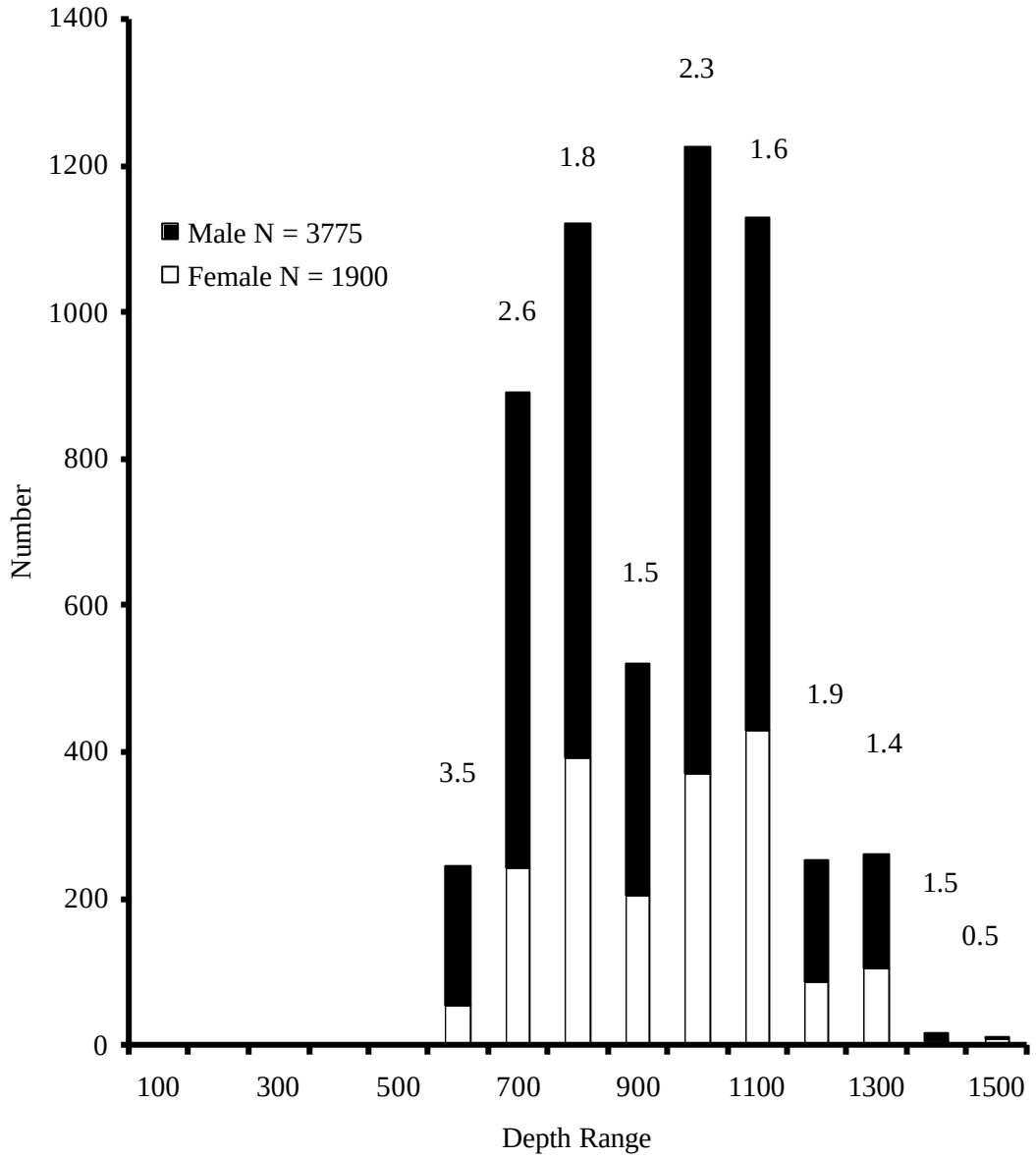


Fig. 3.16. Variation in sex ratio (males: females) by depth range in 100 m intervals for *Deania calcea*. Depth intervals indicated by the upper value in each case.

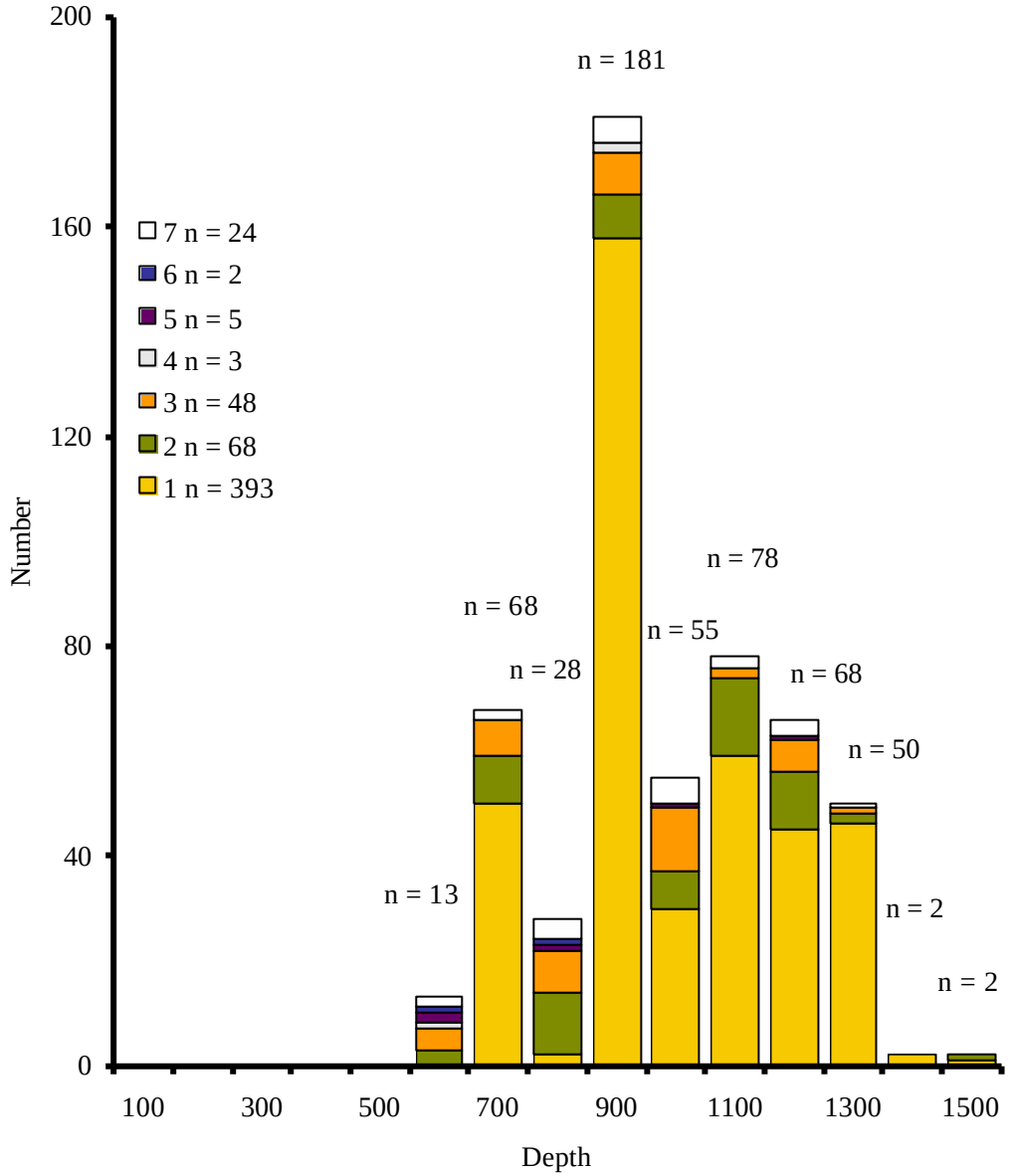


Fig. 3.17. Relative frequencies of maturity stages for female *Deania calcea* by depth range. Depth interval indicated by upper value in each case.

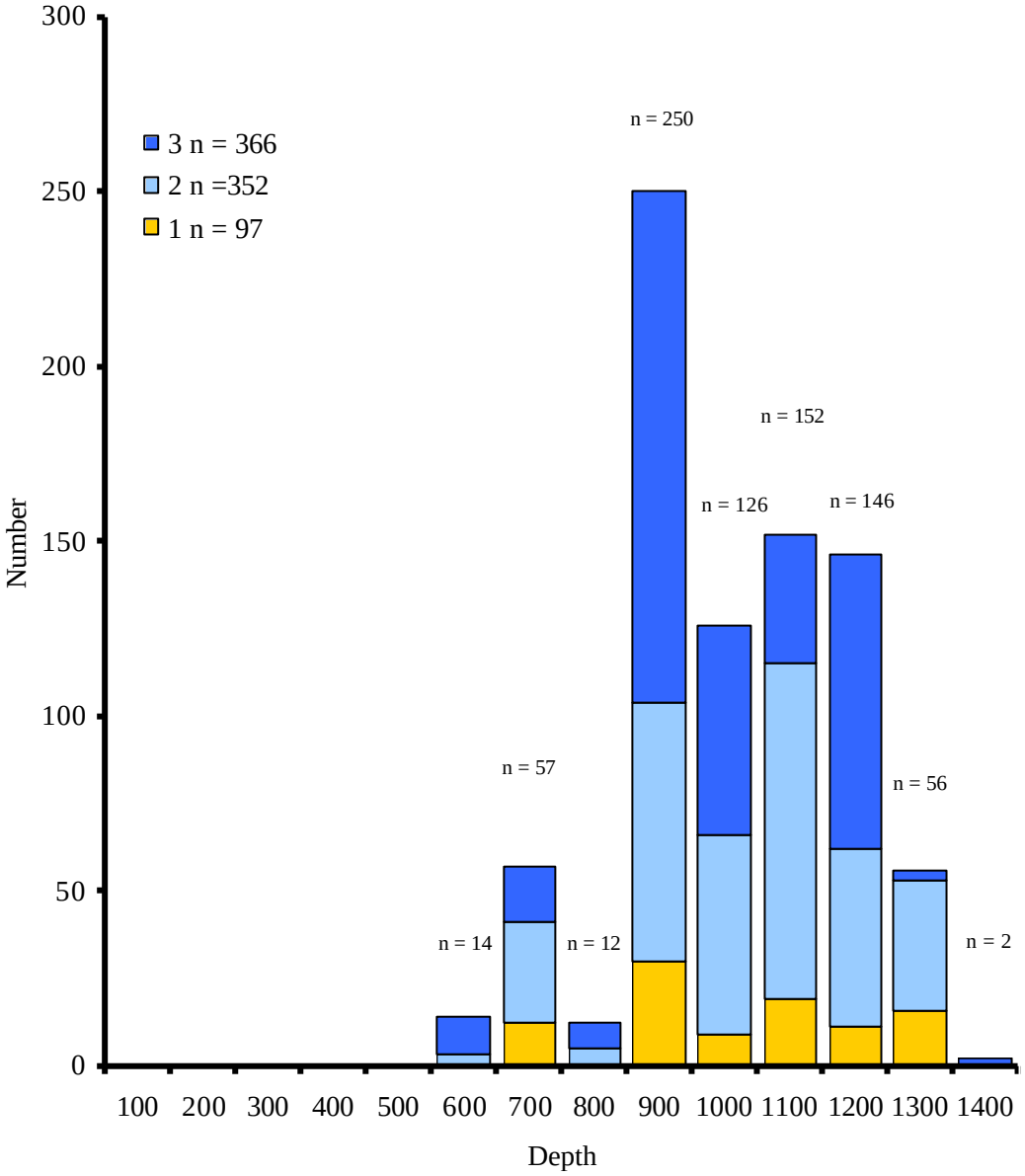


Fig. 3.18. Relative frequencies of maturity stages of male *Deania calcea* by depth range in intervals of 100 m. Depth interval indicated by upper value in each case.

Table 3.5. Frequency of maturity stages by depth interval for female *Deania calceus*.

Depth	Stage 1	Stage 2	Stage 3	Stage 4	Stage 5	Stage 6	Stage 7	Total
500 - 600	0	3	4	1	2	1	2	**13**
600 - 700	50	9	7	0	0	0	2	**68**
700 - 800	2	12	8	0	1	1	4	**28**
800 - 900	158	8	8	2	0	0	5	**181**
900 - 1,000	30	7	12	0	1	0	5	**55**
1,000 - 1,100	59	15	2	0	0	0	2	**78**
1,100 - 1,200	45	11	6	0	1	0	3	**66**
1,200 - 1,300	46	2	1	0	0	0	1	**50**
1,300 - 1,400	2	0	0	0	0	0	0	**2**
1,400 - 1,500	1	1	0	0	0	0	0	**2**
Total	**393**	**68**	**48**	**3**	**5**	**2**	**24**	**543**

Table 3.6. Frequency of maturity stages by depth interval for male *Deania calceus*.

Depth	Stage 1	Stage 2	Stage 3	Total
500 - 600	0	3	11	**14**
600 - 700	12	29	16	**57**
700 - 800	0	5	7	**12**
800 - 900	30	74	146	**250**
900 - 1,000	9	57	60	**126**
1,00 - 1,100	19	96	37	**152**
1,100 - 1,200	11	51	84	**146**
1,200 - 1,300	16	37	3	**56**
1,300 - 1,400	0	0	2	**2**
Total	**97**	**352**	**366**	**815**

Table 3.7. Results of Kolmogorov-Smirnov two sample test for *Deania calcea*.

	Greatest Absolute Difference	Critical Value	Significance
Frequency of males and females	0.375	0.038	S ($p < 0.05$)
Females caught on trawl and long-line from Rockall Trough in 1997	0.362	0.16	S ($p < 0.05$)
Males caught on trawl and long-line in Rockall Trough in 1997	0.774	0.114	S $p < 0.05$

3.1.4 Length frequencies of *Deania calceus*

Length frequencies for the entire study are presented in Fig. 3.19. The length range for females was 52 cm to 119 cm and for males was 55 cm to 109 cm. No specimen smaller than 52 cm TL was recorded in this study. Females attain greater TL than males, though the modal length for females is lower than that for males. The difference in the overall distribution was significant ($p < 0.05$). Table 3.7 presents the results of the K.S. test for comparisons of length frequencies. The populations of each sex had significantly different ($p < 0.05$) distributions. While there was a clear sexual dimorphism in this species, the length frequency distributions differed from those of *Centroscymnus coelolepis*. In the latter species there was a clear separation between modal lengths, while *Deania calceus* length modes were the same for both sexes. These findings accord with the occurrence of maturity stages. Mature, gravid and post-natal female *Centroscymnus coelolepis* were well represented in samples, while *Deania calceus* in this stage of development were largely absent.

Fig. 3.20 shows male and female length frequencies from trawl and long-line in 1997. Trawl and long-line selected for the significantly different ($p < 0.05$) length ranges. Large female *Deania calceus* were well represented in long-line catches, but almost totally absent from trawls, indicating that large females can avoid these nets. Length frequencies by depth are presented in Fig. 3.21. Males showed little evidence of depth segregation by size, but largest females were most numerous between 900 m and 1,100 m.

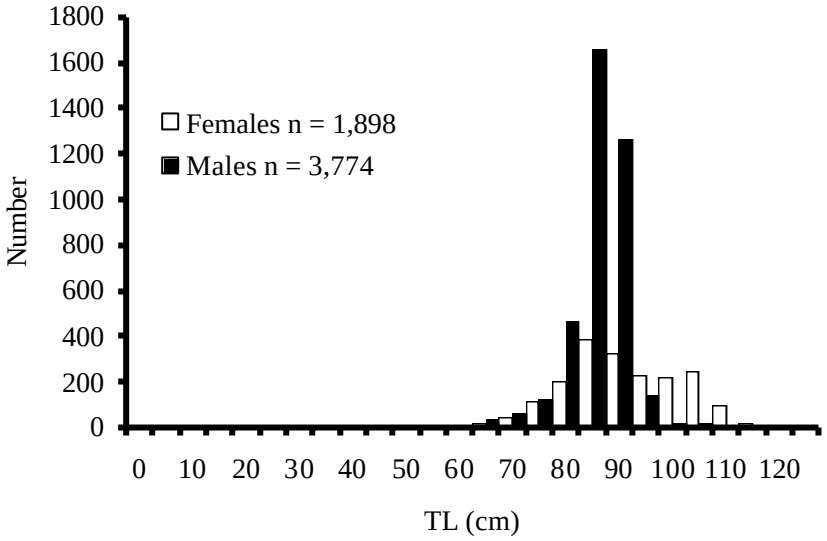


Fig. 3.19. Length frequency for *Deania calcea*, comprising all samples collected during the project.

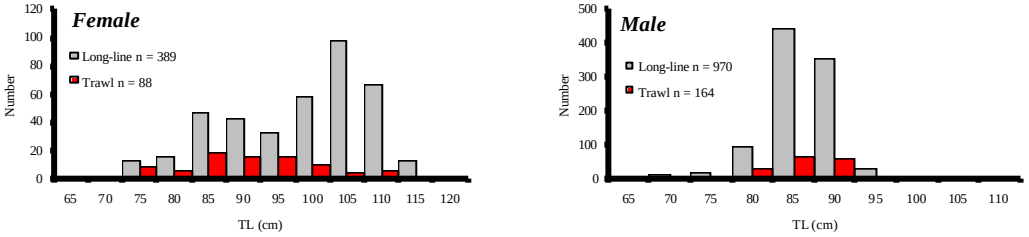


Fig. 3.20. Length frequencies of *Deania calcea* caught on trawl and long-line in the Rockall trough in 1997.

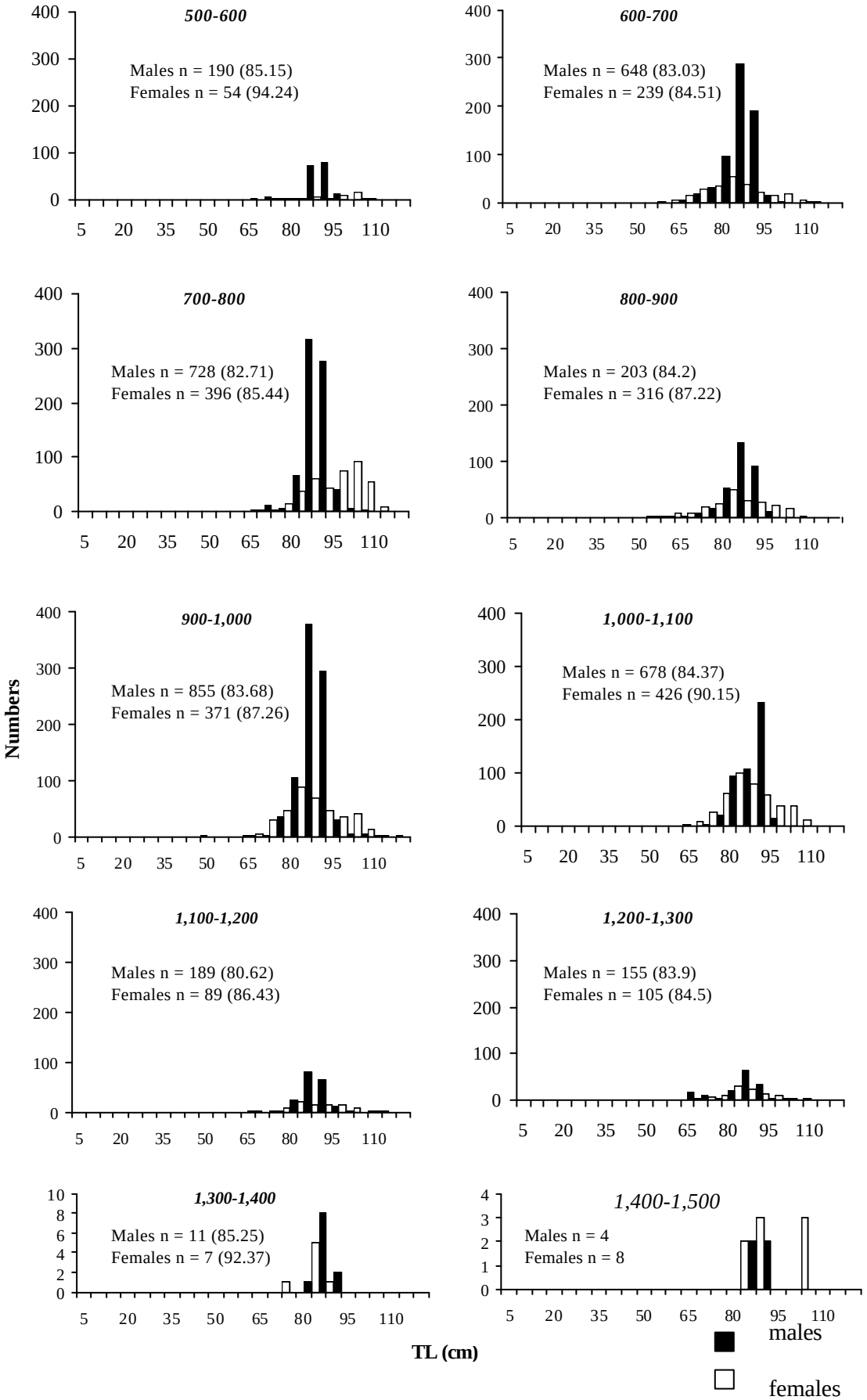


Fig. 3.21. Length frequencies (mean in parenthesis) by depth interval for *Deania calceus*.

3.1.5 Distribution of *Centrophorus squamosus*

CPUE data for trawl and long-line surveys are presented in Fig. 3.22 and Fig. 3.23 respectively. Catch rates for *Centrophorus squamosus* were much higher in the Rockall Trough than on the western or southern Porcupine Slopes with highest catch rates recorded on the Hebrides Terrace. There is some evidence of declines in trawl catches in the Rockall Trough between 1996 and 1997 (Fig. 3.23). Catch rates on the southern slopes of the Rockall Trough were much lower than those of *Deania calceus*, which was very abundant in this area (Fig. 3.12, Fig. 3.13).

Mean CPUE by 100 m depth interval is presented in Fig. 3.24 for trawl and Fig. 3.25 for long-line. The absolute depth range for this species was 610 m – 1,404 m but peak catch rates for *Centrophorus squamosus* on trawl and long-line were taken at 700 and 800 m respectively. The entire depth range of the species in this area of the northeast Atlantic appears to have been sampled, and is within the range of both trawlers and long-liners. The apparent decline in trawl catches may reflect the combined fishing pressure of both gears.

The sex ratio significantly ($p < 0.05$) favoured males generally at shallower depths and significantly favoured females in most deeper waters (Table 3.1). The sex ratios by depth are given Fig. 3.26. In the mid-range of depths approximately equal numbers of each sex were recorded, and as for *Centroscymnus coelolepis* this indicates that mating takes place, to some extent, in this depth range. Unlike that species mature females were infrequent and gravid females totally absent. This is reflected in the sex ratios, which favoured males in lesser depths. Table 3.8 contains the numbers of each female maturity stage by 100 m depth intervals and Fig. 3.27 shows these numbers graphically. Immature, stage 1, females predominated in all depths with maximum numbers between 900 m and 1,100 m. As for the other species mature females were most abundant in the mid-range of depths but none occurred below 1,300 m. Post-natal fish tended to occupy shallower waters than other stages. There was no difference in the frequencies of stages 1 and 2 across the depth ranges sampled. Table 3.9 shows the numbers of male maturity stages by 100 m depth interval. These numbers are presented graphically in Fig. 3.28. There was no obvious depth related

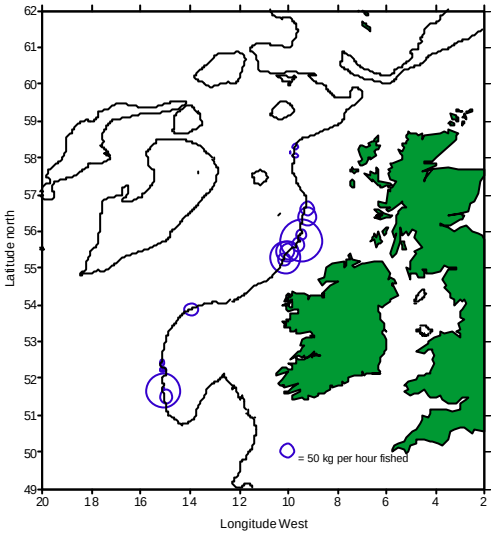
trend in the occurrence of maturity stages among females or males and mature males predominated in all depth ranges.

Table 3.8. Frequency of occurrence of maturity stages by depth interval for female *Centrophorus squamosus*.

Depth	Stage 1	Stage 2	Stage 3	Stage 7	Total
600 - 700	5	0	3	1	**9**
700 - 800	5	0	1	2	**8**
800 - 900	16	2	2	1	**21**
900 - 1,000	129	17	6	7	**159**
1,000 - 1,100	102	7	13	3	**125**
1,100 - 1,200	44	5	1	0	**50**
1,200 - 1,300	38	3	4	3	**48**
1,300 - 1,400	5	0	0	0	**5**
1,400 - 1,500	4	2	0	0	**6**
Total	**348**	**36**	**30**	**17**	**431**

Table 3.9. Frequency of occurrence of maturity stages by depth interval for male *Centrophorus squamosus.*

Depth	Stage 1	Stage 2	Stage 3	Total
600 - 700	0	11	23	**34**
700 - 800	6	11	19	**36**
800 - 900	3	1	28	**32**
900 - 1,000	37	37	106	**180**
1,000 - 1,100	10	18	49	**77**
1,100 - 1,200	1	4	27	**32**
1,200 - 1,300	1	3	20	**24**
1,300 - 1,400	2	5	10	**17**
1,400 - 1,500	1	0	0	**1**
Total	**61**	**90**	**282**	**433**



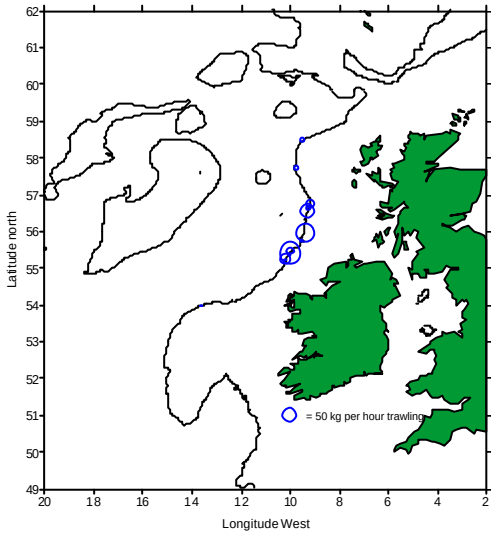
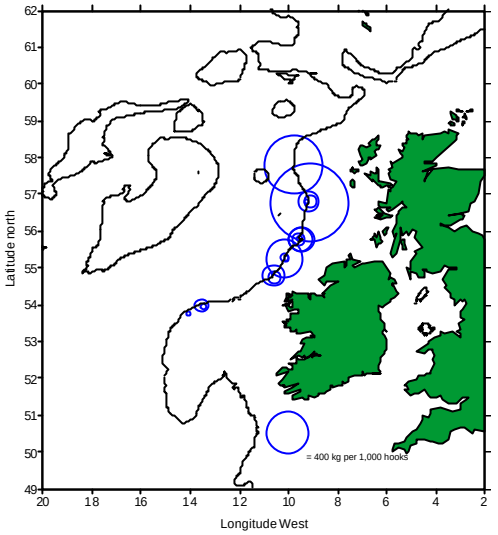


Fig. 3.22. Catch per unit effort of *Centrophorus squamosus* (kg per hour trawling) for September 1996 survey (top) and October – November 1997 survey (bottom). The 1,000 m contour is indicated.



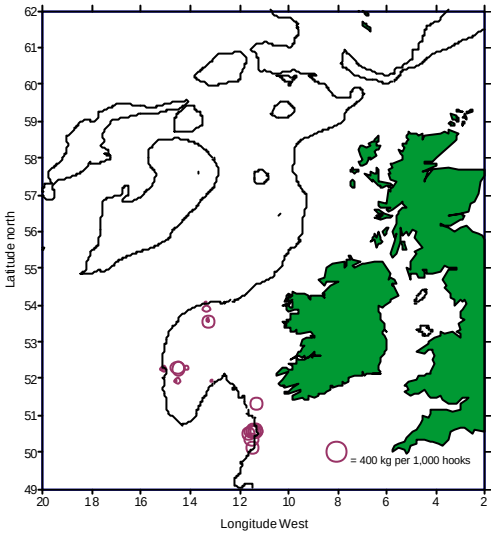


Fig.3.23. Catch per unit effort of *Centrophorus squamosus* (kg per 1,000 hooks) for long-line surveys in August 1997 (top) and December 1999 (bottom). The 1,000 m contour is indicated.

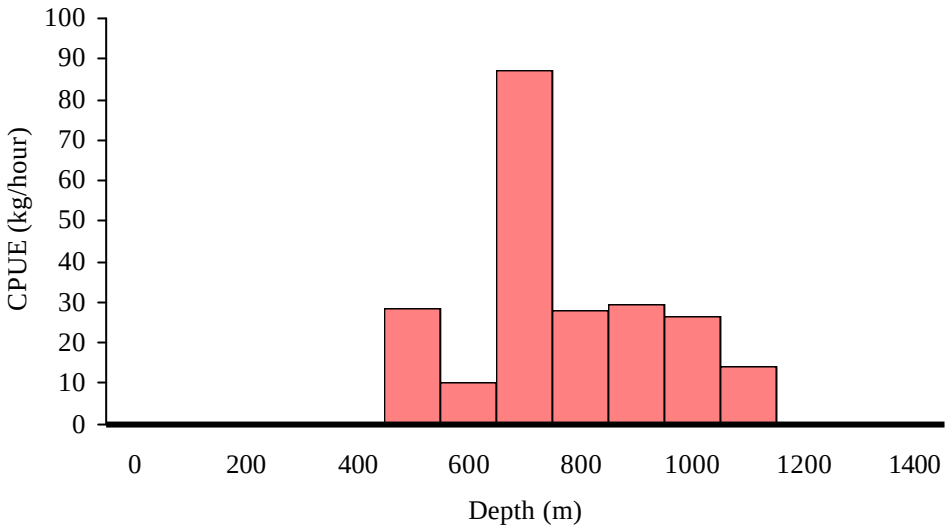


Fig. 3.24. Variation in average CPUE (kg per hour trawled) for *Centrophorus squamosus*, based on trawl surveys in 1996 and 1997. Each 100 m depth interval is indicated by its lower value.

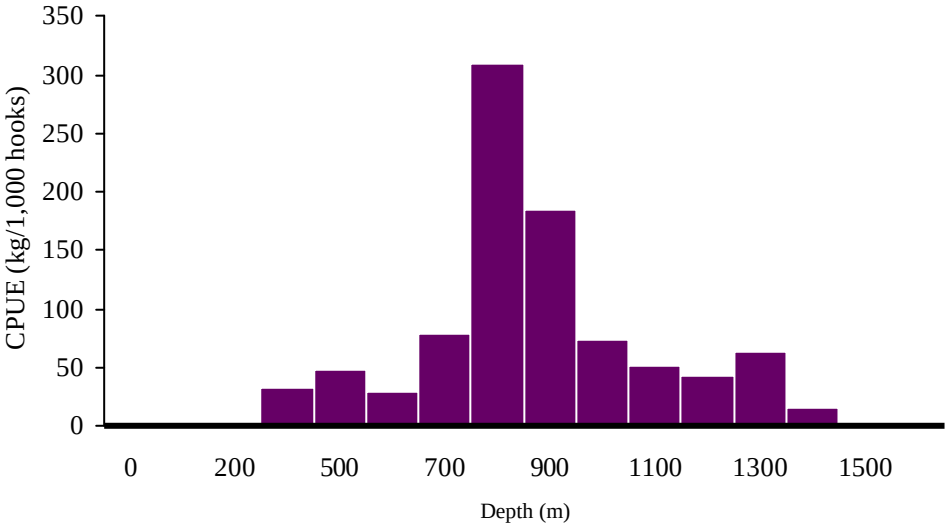


Fig. 3.25. Variation in average CPUE (kg per 1,000 hooks) for *Centrophorus squamosus*, based on long-line surveys in 1997 and 1999. Each 100 m depth interval is indicated by its lower value.

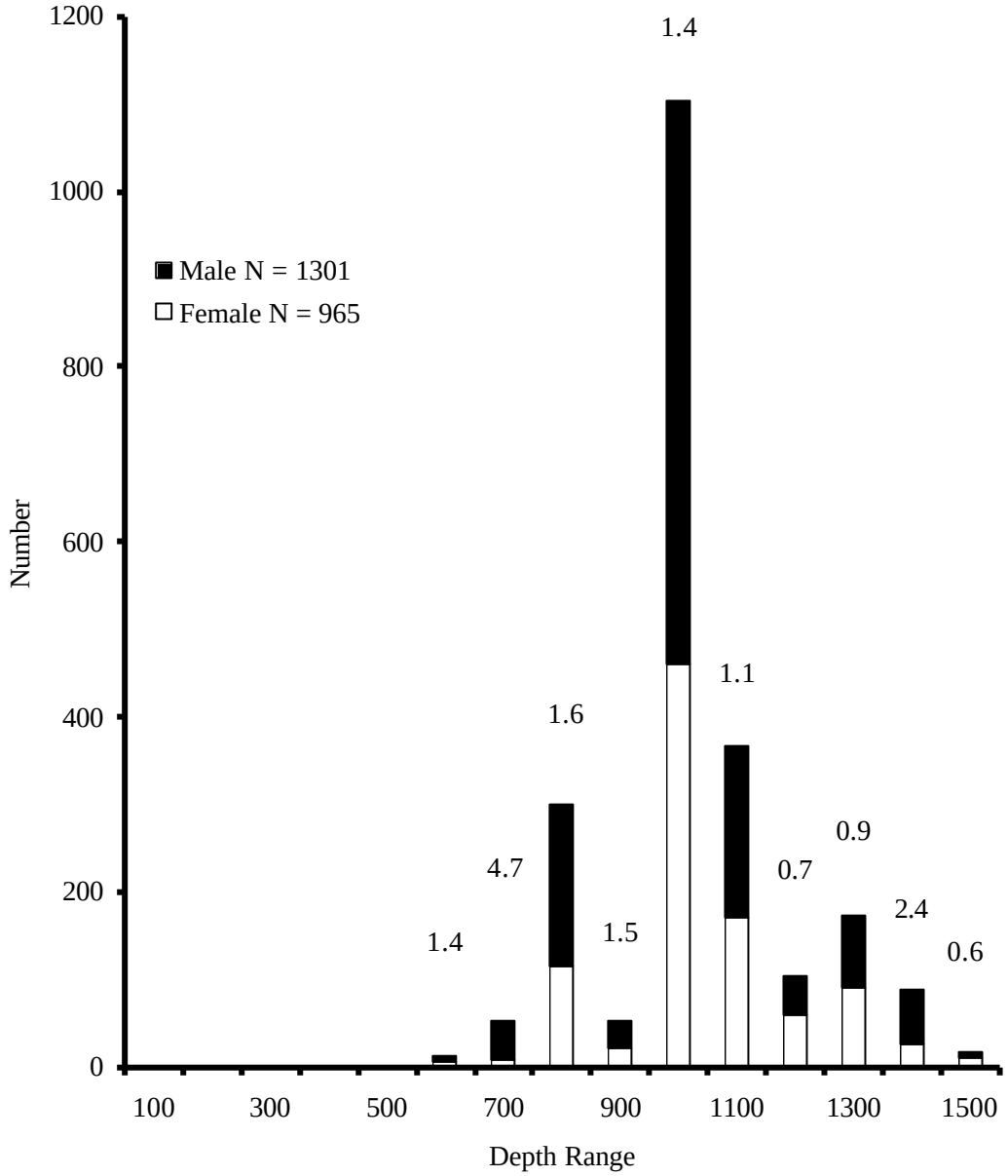


Fig. 3.26. Variation in sex ratio (males : females) with depth range in100 m intervals for *Centrophorus squamosus*. Depth interval indicated by the upper value in each case

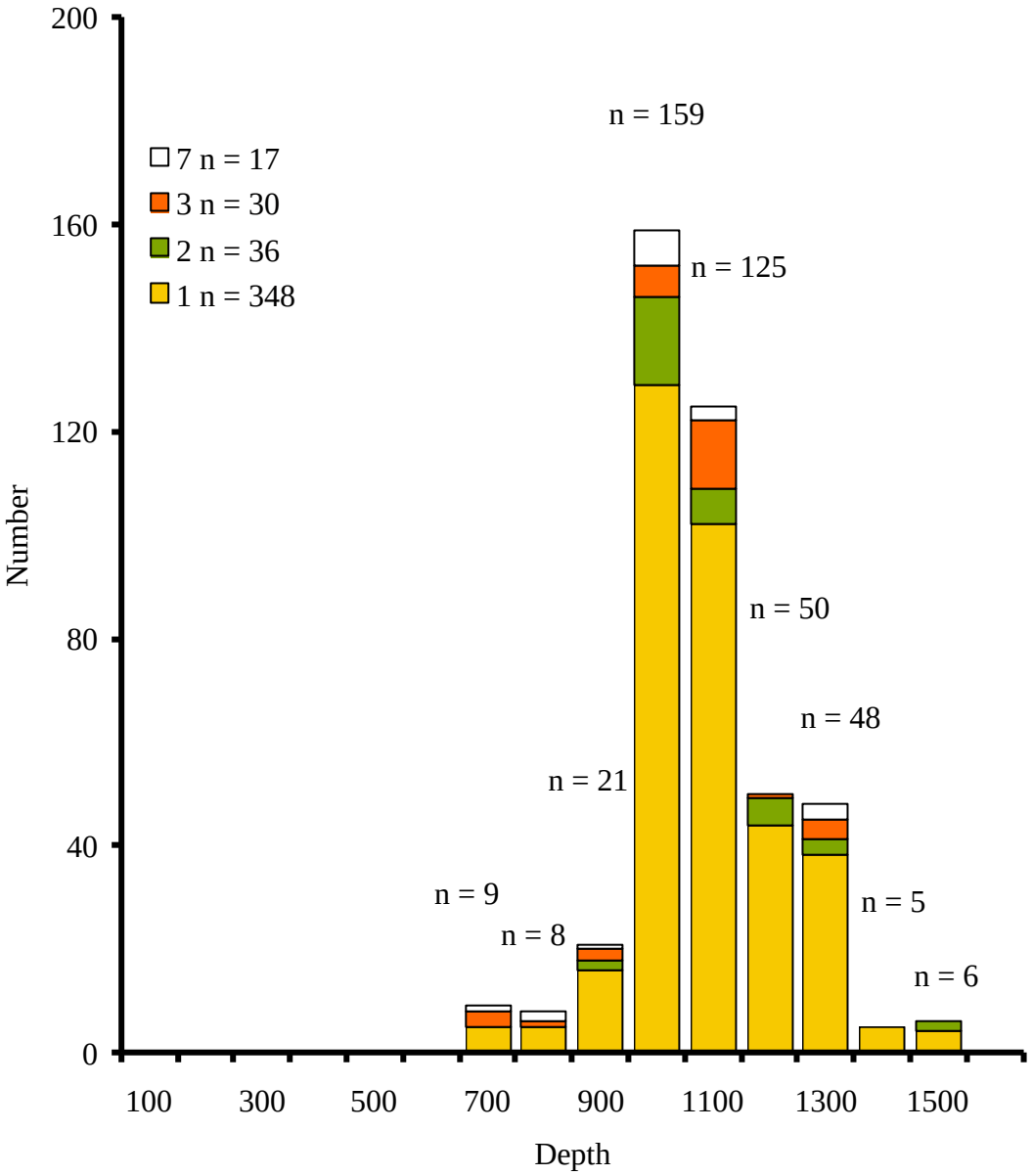


Fig. 3.27. Relative frequency of occurrence of maturity stages of female *Centrophorus squamosus* by depth range in 100 m intervals. Depth interval indicated by upper value in each case.

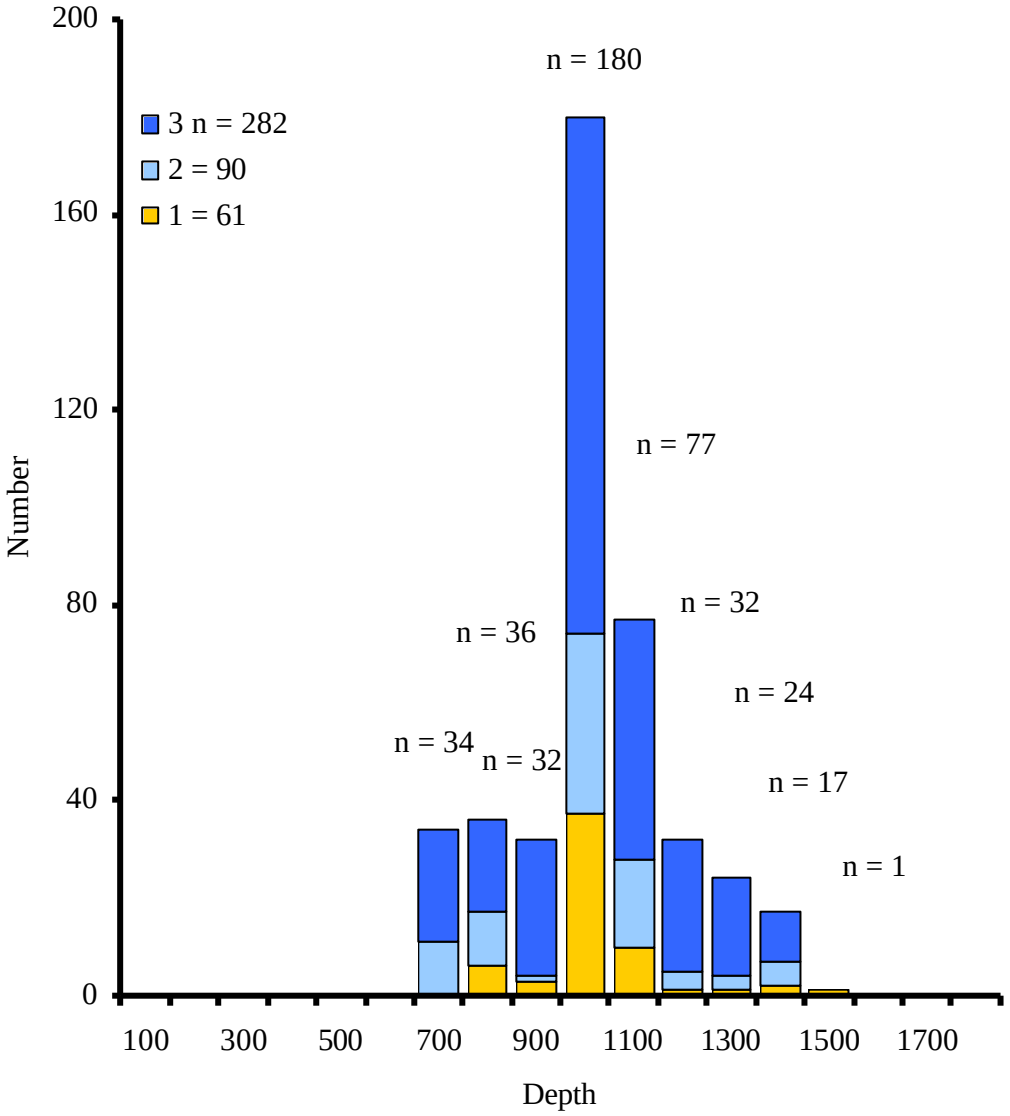


Fig. 3.28. Relative frequencies of occurrence of maturity stages of male *Centrophorus squamosus* by depth range, in 100 m intervals. Depth interval indicated by the upper value in each case.

3.1.6 Length Frequencies for *Centrophorus squamosus*

The smallest length recorded was 80 cm for females and 83 cm for males. The greatest lengths were 122 cm for males and 145 cm for females. The overall length frequencies for males and females are presented in Fig. 3.29. The overall length frequencies for this species indicate sexual dimorphism, with females attaining larger size. However, as for *Deania calceus*, modal lengths were the same for both sexes, in contrast to *Centroscymnus coelolepis* which displayed separated modes. Evidently larger female *Centrophorus squamosus* are mainly absent from this area. Results of the Kolmogorov-Smirnov two-sample test are given in Table 3.10. These results indicate that the sexes were sampled from populations with differing length frequency distributions ($p < 0.05$). Male and female length frequencies from trawl and long-line are compared in Fig. 3.30. The K-S test did not detect significant differences in the distributions for either sex. While long-lines were more efficient at catching *Centrophorus squamosus*, no smaller or larger specimens were taken by either gear. Fig. 3.31 shows length frequencies by sex for each 100 m depth interval. There was little evidence of decreasing size with depth in males, but there was an overall tendency of decreasing female length with depth.

Table 3.10. Results of Kolmogorov-Smirnov two sample test for *Centrophorus squamosus* length frequencies.

	Greatest Absolute Difference	Critical Value	Significance
Frequency of males and females all samples	0.179	0.056	S ($p < 0.05$)
Females caught on trawl and long-line from Rockall Trough (1997)	0.143	0.169	NS
Males caught on trawl and long-line from Rockall Trough (1997)	0.114	0.511	NS

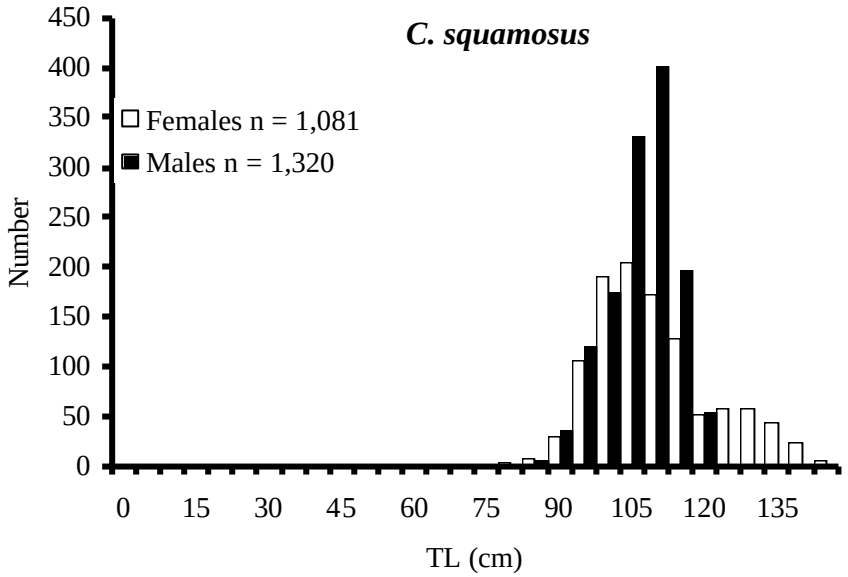


Fig. 3.29. Length frequency for *Centrophorus squamosus* comprising the entire study.

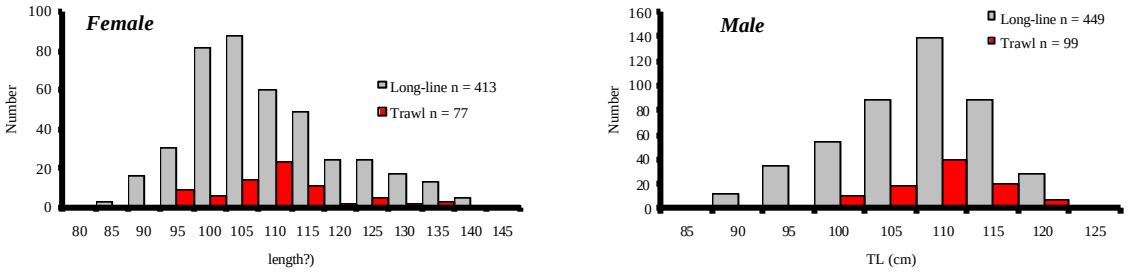


Fig. 3.30. Comparison of length frequencies of trawl and long-line caught *Centrophorus squamosus* from the Rockall trough in 1997.

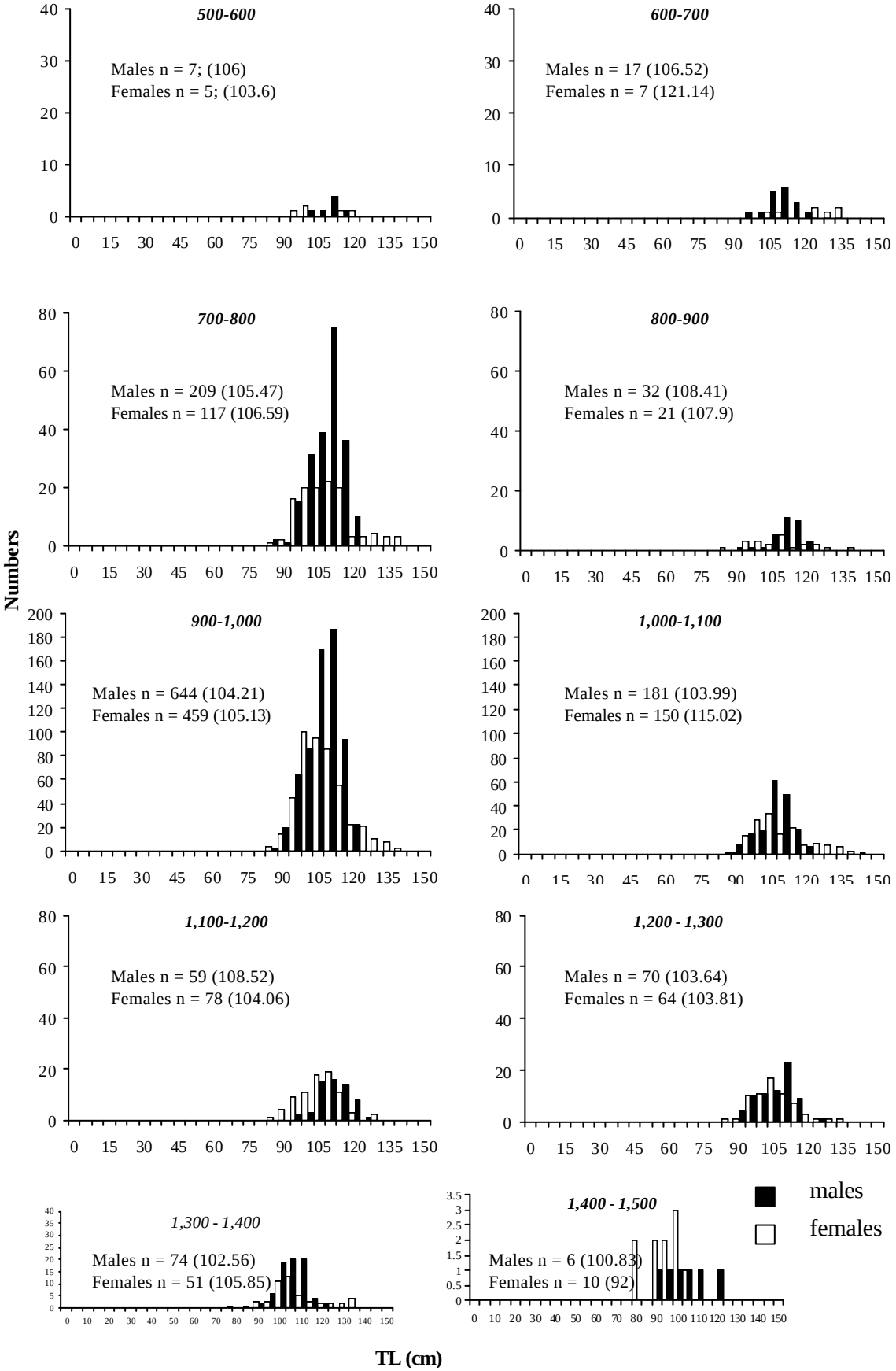


Fig. 3.31. Length frequencies (mean in parenthesis) by 100 m depth increment for *Centrophorus squamosus.*

3.1.7 Discarding

The discard rates were calculated as percentages of the total catch and as kg per tonne of target species. The target species was "siki", the commercial name given to *Centrophorus squamosus* and *Centroscymnus coelolepis* combined. While some of these sharks were discarded during the surveys they were considered as having been landed for the purposes of calculation of discard rates.

The discard rate expressed as a percentage of the total catch for each of the 4 surveys is presented in Table 3.11. The percentage discard rate for *Deania calceus* was greatest on the southern slopes of the Rockall Trough and on the south-western slopes of the Porcupine Bank. This corresponds to areas of peak abundance of the species in catches. Clearly, long-lining in these areas produces large discards of *Deania calceus*. Discarding of this species, as a percentage of total catch was quite low in the trawl surveys. However trawl catches tend to comprise a wide range of species (Connolly and Kelly, 1996). When discarding is expressed as kg per tonne target species ("siki and faux siki") then it becomes apparent that considerable quantities of *Deania calceus* were being discarded. The discard rate in kilogrammes per tonne of target species (*Centrophorus squamosus* and *Centroscymnus coelolepis*) are given in Table 3.12. Highest discards of this species occur on the southern slopes of the Rockall Trough (area 5).

Discarding from French and Scottish trawlers was estimated from the official landed weights from these vessels in 1996. A conversion factor for gutted to round weights was calculated by linear least squares regression analysis as follows;

Round weight (g) = 1.556 * Gutted weight (g) – 122.6

Standard error (S.E.) of the regression coefficient = 0.1974; n = 512; r^2 = 0.924.

Total discarding, in terms of weight and numbers, of *Deania calceus* from trawlers in both the Rockall Trough and the Porcupine Bank, corresponding to the deepwater part of Sub-areas VI and VII where most trawling takes place, is given in Table 3.13. It can be seen that French trawlers account for the greatest proportion of discarding of

Deania calceus. The estimate for Scottish trawlers is probably an overestimate as the landings data for that country comprise all shark species, not deepwater squalid sharks exclusively. The total number of *Deania calceus* estimated to have been discarded in 1996 from trawlers was 285,322 individuals, slightly greater than Connolly and Kelly's (1996) estimate of 256,411. However since the sampling of *Deania calceus* was a priority in the survey upon which the present estimate was based, it is considered to be a more accurate reflection of the numbers discarded.

Percentage discarding of *Deania calceus* for each haul during the December 1999 long-line surveys is presented in Table 3.14. Again the highest discarding occurred on the southern slopes of the Rockall Trough, where over 40 % of the catch was *Deania calceus*. Indeed it accounted for over 30 % of the total catch on the long-line survey of December 1999. However catch rates are depth dependent (Section 3.1.3). Thus long-lining in waters deeper than 1,200 caught only small amounts of *Deania calceus*. However when long-liners are targeting *Centrophorus squamosus*, *Mora moro* and *Phycis blennoides*, in waters less than 800 m, discarding may be as high as 40 %.

Table 3.11. Discard rates for *Deania calceus* expressed as percentages of the total catch by survey area. During 1999 long-line survey the entire catch was sampled.

Survey	Date	Area	Sample kg	Total discard kg	Total catch kg	Discard rate %
Long-line	2nd -12th	2	23	23	2128	1.1
	August 1997	3	56	56	3750	1.5
		4	1206	1206	6556	18.4
		5	2197	3071	6619	46.4
Long-line	30th November -	5	3620	3620	8229	43.0
	10th December 1999	6	2105	2105	7507	28.0
		7	783	783	5478	14.3
		8	2508	2508	6496	38.6
Trawl	16th -26th	1	53	53	2722	1.9
	September 1996	2	12	12	638	1.8
		3	23	23	2099	1.9
		5	67	211	4319	4.8
		6	63	63	13552	0.5
		7	99	99	1704	5.8
Trawl	29th October -7th	1	22	22	2270	1
	November 1997	2	25	25	2421	1
		3	57	57	3856	1.5
		4	80	80	4674	2
		5	431	431	4689	9.2

Table 3.12. Discard rate in kg *Deania calceus* discarded per tonne of deepwater shark landed during 1996 and 1997 surveys.

Survey	FRC Area	*Centrophorus squamosus*	No.	*Centroscymnus coelolepis*	No.	Total Shark	*Deania calceus*	Rate kg / tonne
Sept 96	1	211	4	76	3	287	53	184.60
	2	320	3	24	1	345	12	34.81
	3	163	5	24	1	187	23	122.73
	4	896	4			896		
	5			95	1	95	211	2282.05
	6	430	5	495	5	926	63	68.07
	7	345	3	141	3	486	99	203.75
	8	58	2	40	1	98		0.00
		2424	**26**	**896**	**15**	**3320**	**461**	**138.86**
Oct –Nov 97	1	130	3	163	2	293	22	75.18
	2	305	3	302	3	607	25	41.19
	3	169	3	73	2	242	57	235.76
	4	608	6	60	1	668	80	119.78
	5	1081	3	347	3	1428	431	301.80
		2293	**18**	**944**	**11**	**3237**	**615**	**189.97**
August 1997	2	1407	5	**169**	**2**	1576	23	14.60
	3	1588	4	499	3	2087	56	26.83
	4	2307	9	704	4	3011	1206	400.51
	5	766	8	1201	5	1966	3071	1561.83
		6068	**26**	**2572**	**14**	**8640**	**4356**	**504.16**
Nov-Dec 99	5	1194	6	46	6	1240	3620	2920.29
	6	1513	4	1352	5	2865	2105	743.73
	7	1281	6	2052	6	3333	783	234.91
	8	629	19	847	19	1476	2508	1699.3
		4617	**35**	**4297**	**36**	**8914**	**9016**	**1011.44**
Both long-line surveys		**10685**	**61**	**6869**	**50**	**17554**	**13372**	**761.76**

Table 3.13. Estimates of total discards from trawlers of *Deania calceus* in the Rockall trough and Porcupine slopes in 1996.

Fleet	Discard Rate Kg / tonne target species	Landings t gutted	Landings t round	Discard t	Discard numbers
French only	138.86	3,284	5,281	733	280,386
Scottish	138.86	55	86	12	4,572
French and Scottish	138.86	3,339	5,367	745	285,322

* Numbers discarded were based on an average weight of 2.612 kg per individual sampled on the 1996 survey

Table 3.14. Percentage discard rates during long-line survey in December 1999 for *Deania calceus*.

Area	Haul	Depth m	Discards kg	Total Catch kg	Discard rate %
5	1	988	1210	2555	47.4
5	2	748	768	1401	54.8
5	3	557	520	1087	47.8
5	4	1277	93	480	19.3
5	6	745	1029	1644	62.6
6	8	585	22	604	3.7
6	9	765	514	856	60.1
6	10	944	535	1572	34.1
6	11	1097	990	2491	39.8
6	12	1304	23	935	2.5
6	13	1378	19	1049	1.8
7	14	1227	67	1002	6.6
7	15	1038	174	653	26.6
7	16	907	453	1333	34.0
7	17	1403	10	867	1.2
7	18	695	9	640	1.4
7	19	1209	70	983	7.1
8	20	1251	356	694	51.2
8	21	610	600	1041	57.7
8	22	883	852	1124	75.8
8	28	1444	22	312	7.0
8	30	1032	23	155	15.0
8	31	849	6	102	5.7
8	32	995	22	204	10.6
8	33	988	132	435	30.4
8	34	1105	135	351	38.4
8	35	1071	106	742	14.3
8	36	1071	127	527	24.0
8	38	1125	129	264	48.9

3.2 Reproduction

The scale used in the present study made use of several criteria for assessing the state of maturity. In males, the length and hardness of the claspers was taken into consideration, along with testis width, development, size and the condition of the *vas deferens*. For females the presence, size and number of oocytes were used to assess maturity, along with the width and condition of the uteri. Only in the case of female *Centrophorus squamosus* did this scale prove difficult to use.

3.2.1 Reproductive cycle and Maturity in *Centroscymnus coelolepis*

The maturity stages of *Centroscymnus coelolepis* are illustrated in Plates 3.1 to Plate 3.6. Males possessing tiny, undeveloped claspers and thread-like testes were assigned to stage 1 (Plate 3.1), while those with soft, developing claspers, enlarged testes and meandering sperm ducts were assigned to stage 2. Stage 3 (mature) specimens were defined as those with stiff claspers and thickened, convoluted testes. The variation in testis width with TL is shown in Fig. 3.32. It is clear that the testes undergo an abrupt increase in width between stages 1 and 2. The testes, however, never return to stage 1 dimensions. Nevertheless there was not much appreciable difference between the widths of stage 2 and stage 3 testes. Right and left testes did not have significantly different widths (paired samples t-test, $p > 0.4$) therefore width data were pooled across both left and right organs. Widths for stage 1 testes were not included in data analysis because they had a different range of the covariate (TL). Covariate (TL) by factor (maturity stage) interaction was not significant ($p > 0.2$) so ANCOVA was developed to test for significant differences in mean testis width adjusted for mean TL. Results of ANCOVA of testis data are contained in Table 3.15. Results of ANCOVA showed that there was no significant difference ($p > 0.2$) in testis width between stage 2 and stage 3. The mean values on normal (anti-logged) scale are presented in Table 3.16. As the testes also became convoluted with maturity the change in testis weight was measured throughout the maturation process.

Testes also became convoluted at stage 3, presumably to more easily accommodate an increase in the volume of the organ in the limited space available. To investigate the development of the testes throughout the maturation process testes weight was

analysed by regression and ANCOVA. The interaction of the covariate (TL) and factor (maturity stage) was not significant ($p > 0.1$), therefore ANCOVA was developed to test for significant differences in mean testes weight by maturity stage, adjusting for the mean covariate (TL), see Table 3.15. Results of ANCOVA indicate that the effect of maturity was significant ($p < 0.01$). Gabriel's approximate method was employed to test for significant differences among the adjusted mean testes weights for each maturity stage, the results of these comparisons are contained in Table 3.17 and presented graphically in Fig. 3.36. The results of these pair-wise comparisons show that mean weight of stage 1 testes was significantly less than for the other stages. Mean weight of stage 2 and 3 testes were not significantly different however (Fig. 3.36).

Female *Centroscymnus coelolepis* assigned to stage 1 (Plate 3.2) had narrow, thread-like uteri, but an abrupt increase in uterine width ensues (Fig. 3.34). Females in stage 1 had whitish granular ovaries in which no large oocytes were present. Stage 2 specimens had differentiating oocytes in their ovaries and stage 3 had one dominant population of ripe oocytes. In stages 2 and 3 (Plate 3.3) the uterine width increased markedly. After ovulation the uteri became candled to accommodate undifferentiated yolk (Plate 3.4). Maximum width was achieved at stage 6 (Plate 3.5), when the females were carrying near-term embryos, however by stage 7 the uteri had returned to their pre-ovulatory size (Plate 3.6). Width data for stages 2, 4, and 6 of the females were eliminated from further analysis because of small sample sizes. Covariate (TL) by factor (maturity stage) interaction was not significant ($p > 0.7$) so ANCOVA was developed to test for significant differences in mean uterus width, after adjusting for mean TL. ANCOVA found heterogeneity of adjusted mean uterus width ($p < 0.01$).
Gabriel's approximate method was used to test for significant differences among uteri at each stage of maturity and results are contained in Table 3.17 and presented graphically in Fig. 3.37. Adjusted mean uterus width of stage 5 females was significantly greater ($p < 0.05$) and the adjusted mean uterus width of stage 1 females, significantly less ($p < 0.05$) than of other stages. However mean uterus widths for stages 3 and 7 females were not significantly different. It seems reasonable to conclude that post-natal uteri return quickly to their pre-gravid dimensions, as illustrated by comparison of Plates 3.3 and 3.6.

The maturity scale was considered adequate for the purposes of assessing maturity in the population, since it was based on presence of ripe sex products and the condition of the reproductive tract and secondary sexual characteristics. Table 3.18 presents the proportions of males and females mature in each length class. In female *Centroscymnus coelolepis* there was an overall tendency for increased maturity with successive length increments. The proportion of mature male *Centroscymnus coelolepis* did not increase with every successive length increment. The results of Probit modelling of the proportions mature are given in Fig. 3.38 for females and Fig. 3.39 for males, and the results of Probit analysis are contained in Table 3.19. Female TL_{50} estimated by Probit analysis was 102.5 cm. In the case of males while the greatest proportion mature was reached at 91 cm, 100 % maturity was not achieved at any length. Estimated TL_{50} was 86.4 cm for males. Males attained sexual maturity at a smaller proportion (79 %) of maximum length than females (85 %), but in both cases maturity was only attained at a large size (Table 3.19).

The variation in the frequency of female maturity stages by quarter is given in Fig. 3.40. There was some variation in the percentage frequency of occurrence of maturity stages between quarters (seasons), with most post-natal sharks recorded in December. However, all stages of the female reproductive cycle were recorded in each period of the year. There does not appear to be any obvious seasonal reproductive cycle, or a predominance of females of any maturity stage at particular times of the year.

Table 3.15. Mean organ width by maturity scale at mean TL based on analysis of covariance of organ width and maturity stage on TL,. Both TL and organ width logarithmically transformed except where indicated thus*.

Species	Organ	Stage	Mean	S.E.	n	95% C.I.	
						Lower	Upper
C. coelolepis	uterus	**1**	1.19	0.0548	58	1.082	1.299
	width	**3**	2.816	0.0483	39	2.72	2.911
		5	4.025	0.0635	23	3.9	4.151
		7	2.942	0.0429	52	2.857	3.026
			Evaluated at covariate (ln TL) = 4.618.				
C. squamosus	uterus	**3**	3.198	0.0335	47	3.131	3.265
	width	**7**	3.316	0.0490	22	3.218	3.414
			Evaluated at covariate ln (TL) = 4.874				
C. squamosus	testis	**2**	2.457	0.0594	31	2.339	2.574
	width	**3**	2.746	0.0287	110	2.69	2.803
			Evaluated at covariate (ln TL) = 4.679.				
C. coelolepis	testis	**2**	2.835	0.032	54	2.772	2.898
	width	**3**	2.883	0.0199	139	2.844	2.923
			Evaluated at covariate (ln TL) = 4.508.				
C. coelolepis	testis	**1**	1.017	0.0938	8	0.831	1.203
	weight	**2**	3.803	0.0418	29	3.72	3.885
		3	3.775	0.0277	65	3.72	3.83
			Evaluated at covariates Ln (TL) = 4.505				

Table 3.16. Mean and 95 % confidence intervals of mean organ width/ weight by maturity stage at mean covariate (TL) on antilogarithmic scale.

Species	organ measurement	Stage	Mean	n	95 % C.I. Lower	95 % C.I. Upper
C. coelolepis	uterus	**1**	3.288	58	2.951	3.664
	width	**3**	16.705	39	15.185	18.377
		5	55.993	23	49.391	63.476
		7	18.947	52	17.407	20.623
C. squamosus	uterus	**3**	24.481	47	22.898	26.173
	width	**7**	27.546	22	24.979	30.377
C. squamosus	testis	**2**	11.666	31	10.373	13.119
	width	**3**	15.587	110	14.726	16.498
C. coelolepis	testis	**2**	17.031	54	15.988	18.141
	width	**3**	17.873	139	17.184	18.59
C. coelolepis	testis	**1**	2.765	8	2.295	3.33
	weight	**2**	44.814	29	41.251	48.685
		3	43.612	65	41.279	46.078

Table 3.17. Comparisons of organ width / weight by maturity stage by Gabriel's approximate method. Value refers to mean width (logarithmic scale) calculated at mean covariate (ln TL) for *C. coelolepis*. Regression coefficient of allometric function is the value for *C. squamosus.*

Species	organ width	stage	value	S.E.	95 % Co. I	
					lower	upper
C. coelolepis	uterus	**1**	1.19	0.0548	0.918	1.463
		3	2.816	0.0483	2.557	3.074
		5	4.025	0.0635	3.724	4.327
		7	2.942	0.0429	2.7	3.184
C. squamosus	uterus *	**2**	-1.14	1.024	-2.271	-0.009
		3	1.736	0.672	0.824	2.648
		7	1.587	1.591	0.151	3.023
C. coelolepis	testis	**1**	1.017	0.0938	0.638	1.395
	weight	**2**	3.803	0.0418	3.573	4.032
		3	3.775	0.0277	3.591	3.960

Table 3.18. Numbers and proportions mature by length increment for *Centroscymnus coelolepis*.

Females				Males			
TL (cm)	Total	Mature	Proportion Mature	TL (cm)	Total	Mature	Proportion Mature
71	1	0	0.00	70	4	0	0.00
73	1	0	0.00	72	1	0	0.00
74	2	0	0.00	74	2	0	0.00
75	5	0	0.00	75	1	0	0.00
77	1	0	0.00	76	5	0	0.00
78	7	0	0.00	78	2	0	0.00
79	1	0	0.00	79	2	0	0.00
80	4	0	0.00	80	4	0	0.00
81	1	0	0.00	81	4	0	0.00
82	5	0	0.00	82	4	0	0.00
83	5	0	0.00	83	6	1	0.17
84	5	0	0.00	84	4	3	0.75
85	5	1	0.20	85	7	3	0.43
86	4	0	0.00	86	14	9	0.64
87	8	0	0.00	87	24	16	0.67
88	2	0	0.00	88	38	19	0.50
89	1	0	0.00	89	37	26	0.70
90	6	0	0.00	90	40	28	0.70
91	6	0	0.00	91	49	38	0.78
92	2	0	0.00	92	68	41	0.60
93	3	0	0.00	93	47	43	0.91
94	6	2	0.33	94	40	30	0.75
95	7	0	0.00	95	38	27	0.71
96	3	0	0.00	96	20	14	0.70
97	6	0	0.00	97	9	5	0.56
98	6	0	0.00	98	10	7	0.70
99	7	1	0.14	99	6	4	0.67
100	16	3	0.19				
101	10	3	0.30				
102	17	7	0.41				
103	16	9	0.56				
104	25	14	0.56				
105	31	19	0.61				
106	32	25	0.78				
107	42	29	0.69				
108	39	32	0.82				
109	37	30	0.81				
110	26	22	0.85				
111	26	23	0.88				
112	19	16	0.84				
113	39	30	0.77				
114	30	28	0.93				
115	13	12	0.92				
116	7	5	0.71				
117	7	7	1.00				
118	3	3	1.00				
119	1	1	1.00				
121	1	1	1.00				

3.2.2 Fecundity in *Centroscymnus coelolepis*

The relationship between number of ripe ova and embryos and TL is illustrated in Fig. 3.41. There was little evidence of increasing ovarian or uterine fecundity with increasing TL, though larger females appeared to produce more oocytes and embryos. In many cases only one uterus was found to contain full term pups, probably due to stress induced parturition. Counts from such females with only one uterus containing pups were not considered. Total counts of ripe oocytes (ovarian fecundity) ranged from 10 to 21, mean = 13. Counts of near-term embryos (uterine fecundity) ranged from 8 to 21, mean = 13. Therefore, while there was some evidence that uterine fecundity was lower than ovarian fecundity the mean and maximum fecundity in each case was the same. Mean length of near-term embryos was 30.7 cm. However, it is unclear how close to parturition these embryos were, despite having absorbed their external yolk sacs.

In a small number of cases, ova were found in the peritoneal cavity. However, no females were ever recorded with partly "candled" uteri and ripe ova in the ovaries suggesting that ovulation takes place relatively quickly. During gestation the ovaries are flaccid and *corpora lutea* were present. Fig. 3.42 illustrates the relationship between the development of oocytes in the ovaries and the width of the uteri. After parturition the oocytes begin to develop again in the ovaries, and subsequent batches of ripe oocytes were produced.

3.2.3 Spermatogenesis in *Centroscymnus coelolepis*

Mean numbers of each spermatogenic stage for immature (stage 2) testes are presented in Table 3.20 and for mature (stage 3) specimens in Table 3.21. Testes from stage 2 males contained all stages of spermatogenic development. However the numbers of ripe and evacuated spermatocysts were small in comparison with stage 3 individuals. As already demonstrated most testicular growth takes place in stage 1 and stage 2 males, with little further development thereafter. This agrees with the results of the analysis of spermatogenesis. However no cross-sections of stage 1 individuals contained any ripe or evacuated spermatocysts.

The relative frequencies of each spermatogenic stage by month are presented in Fig. 3.43. All stages of spermatogenesis were present in the testes from all months sampled. There was no apparent change in the frequency of any stage of spermatogenesis across the sampling period, nor was there any apparent change in the monthly frequencies of each spermatogenic cells by month. There was no significant difference between mean counts of ripe spermatocysts between monthly samples (ANOVA, $p > 0.6$). Thus there was little evidence of a defined seasonal cycle of reproduction in males.

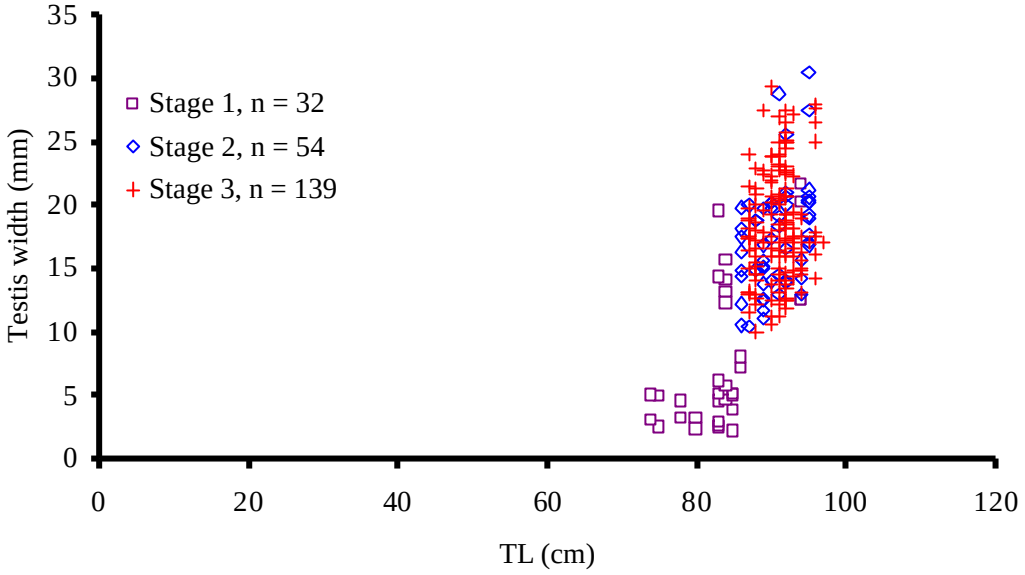


Fig. 3.32. Variation in testis width by maturity stage with total length for *Centroscymnus coelolepis.*

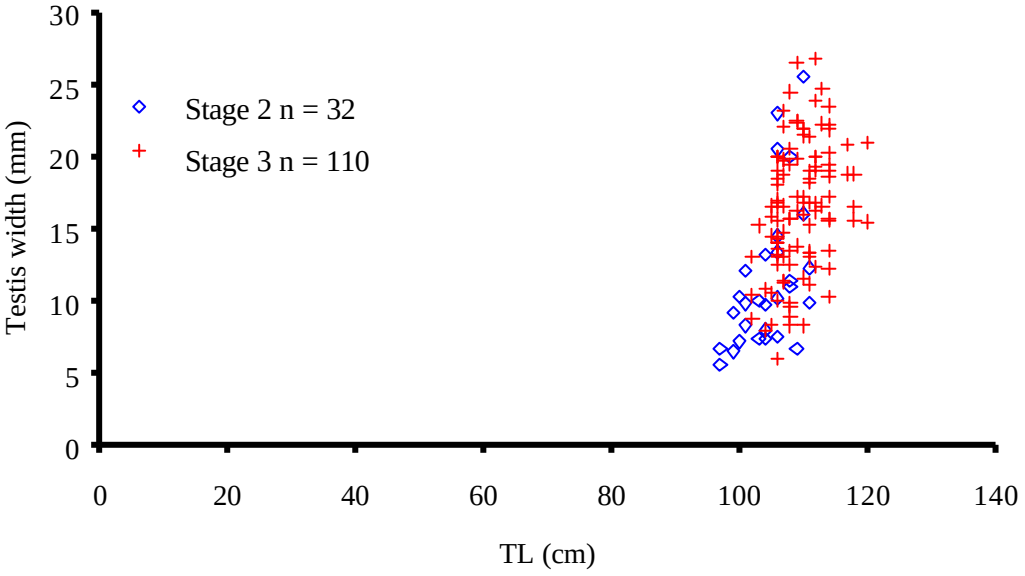


Fig. 3.33. Variation in testis width by maturity stage with total length for *Centrophorus squamosus.*

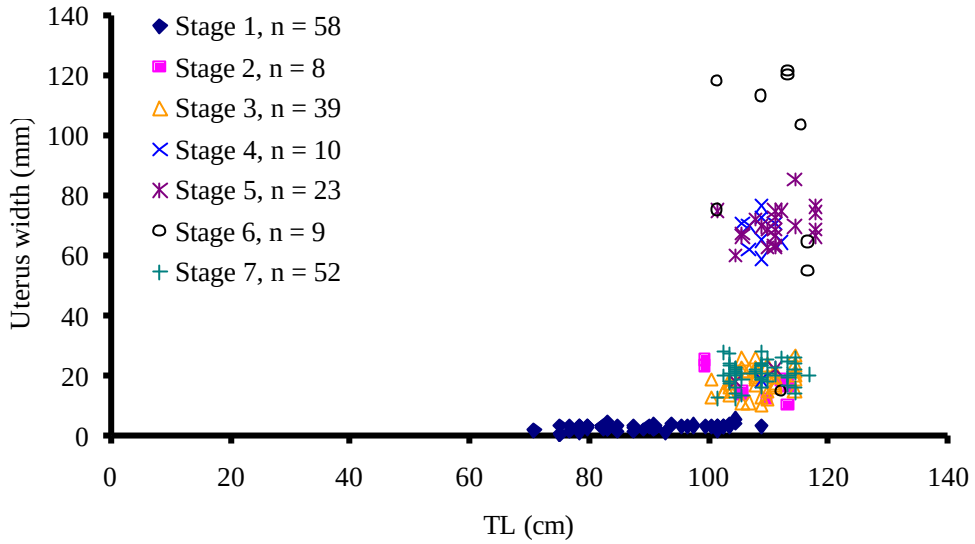


Fig. 3.34. Variation in uterus width by maturity stage with total length for *Centroscymnus coelolepis.*

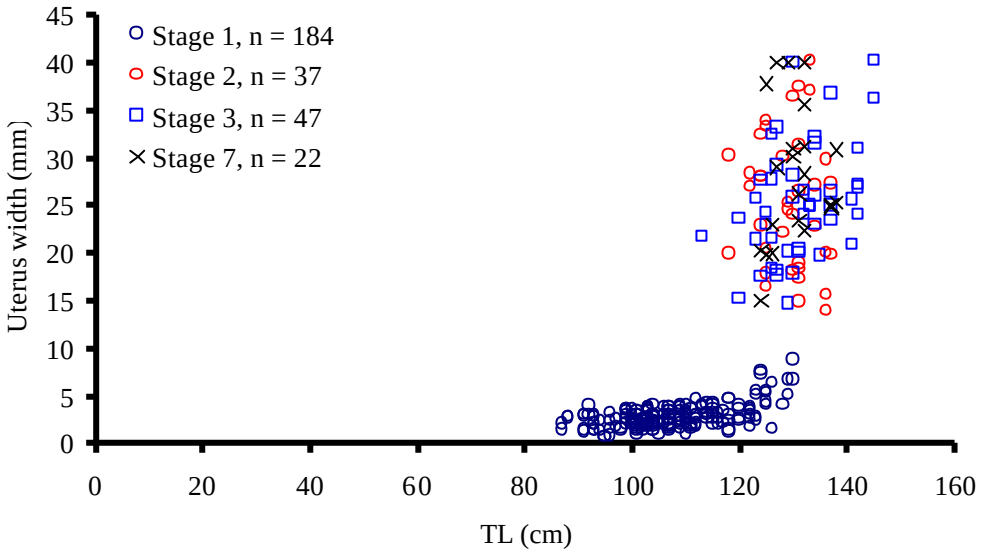


Fig. 3.35. Variation of uterus width by maturity stage with total length for *Centrophorus squamosus.*

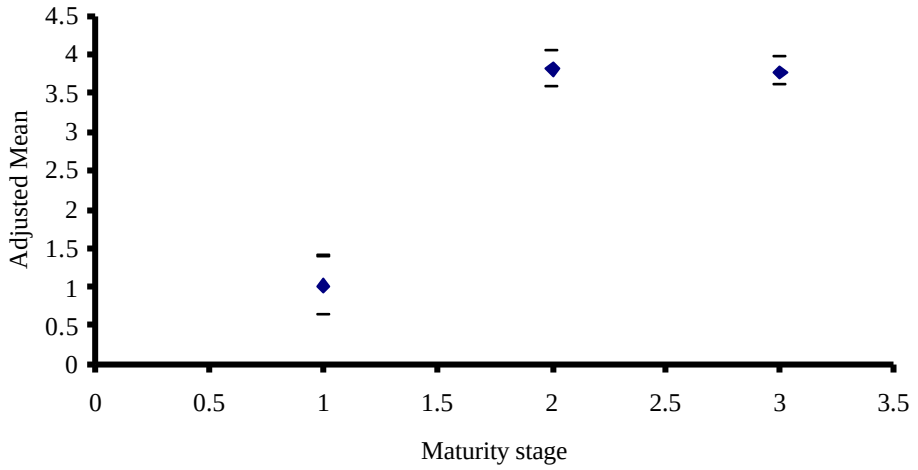


Fig. 3.36. Comparison of mean testis weight adjusted for mean of the covariate (TL) for *Centroscymnus coelolepis*. The GT2 method yielded the 95 % comparison intervals.

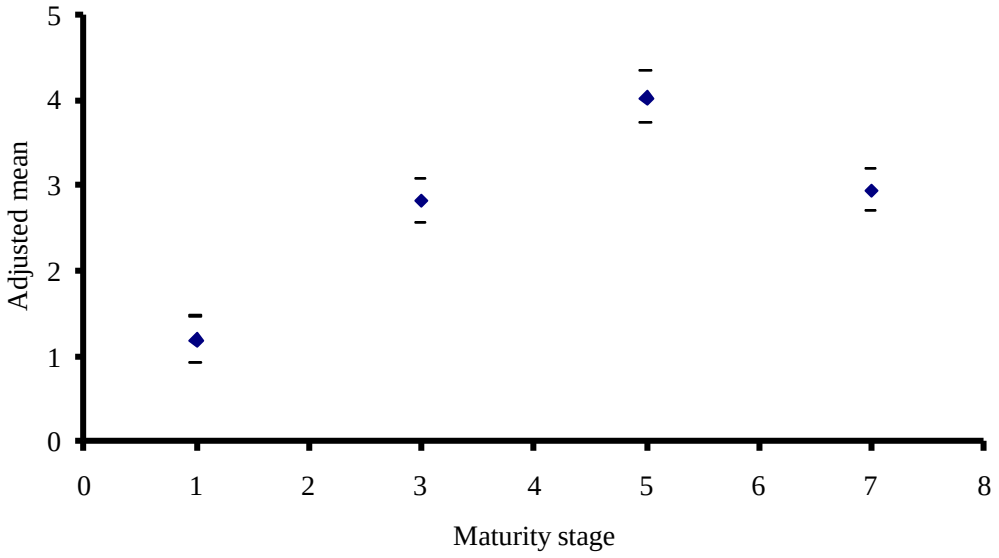


Fig. 3.37. Comparisons of mean uterus width at mean TL (logarithmic scales) by maturity stage for *Centroscymnus coelolepis* by Gabriel's approximate method.

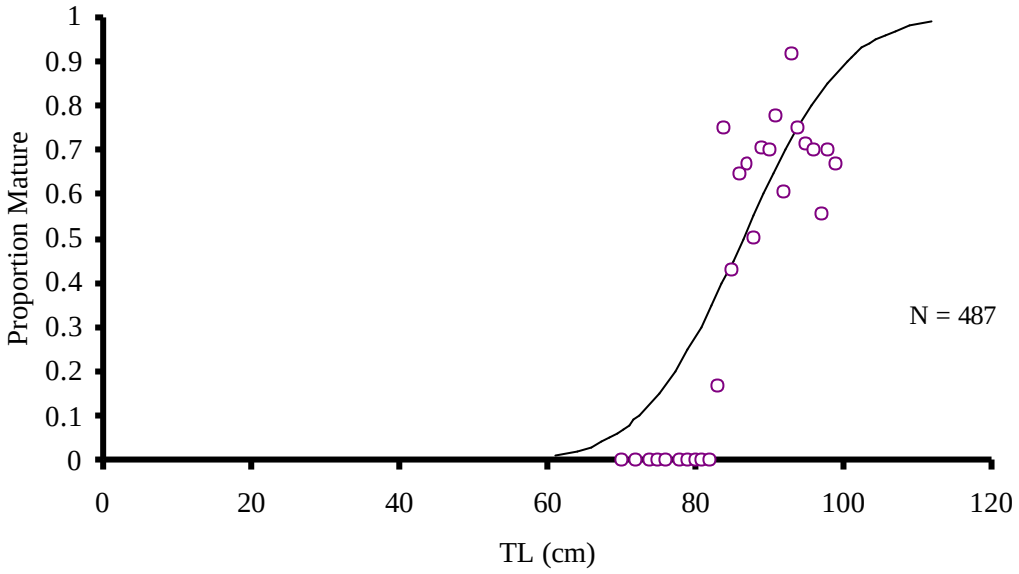


Fig. 3.38. Maturity ogive for male *Centroscymnus coelolepis* fitted by probit analysis. TL at 50 % maturity in the sampled population 87 cm.

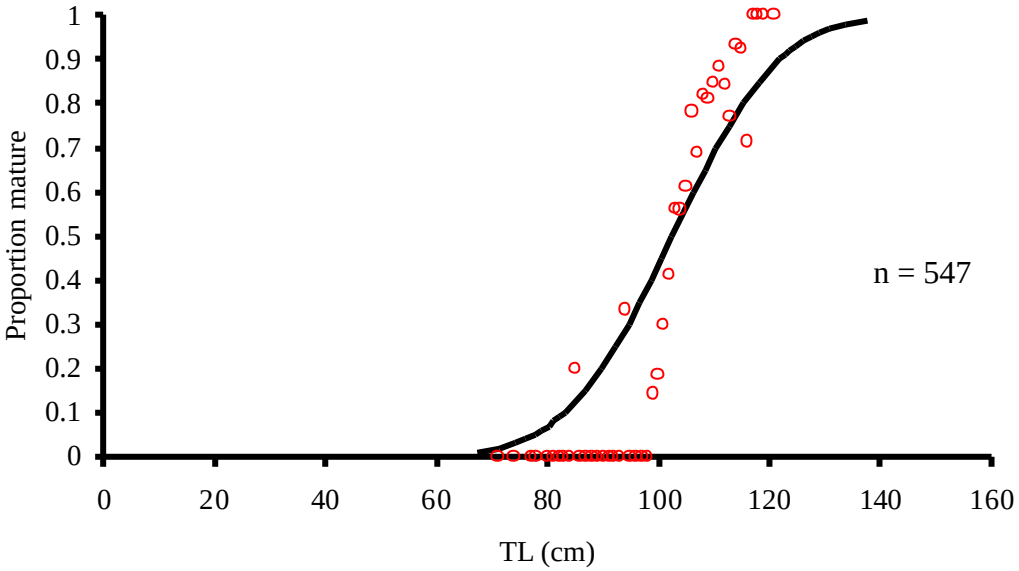


Fig. 3.39. Maturity ogive for female *Centroscymnus coelolepis* fitted by probit analysis. TL at 50 % maturity in the sampled population 102 cm

Table 3.19. Results of Probit analysis of maturity showing estimated length (cm) at 50 % maturity (TL_{50}). Maximum length is given in each case and the ratio of length at 50 % maturity to the maximum.

Species	Sex	TL_{50}	95 % C. I.		Maximum Length	Ratio
			Lower	Upper		
C. coelolepis	female	102.5	97.79	105.73	121	0.85
C. coelolepis	male	86.4	82.48	88.44	109	0.79
D. calceus	female	105.03	102	109.54	119	0.86
D. calceus	male	85.16	83.86	86.74	109	0.78
C. squamosus	female	128.27	126.2	130.7	145	0.88
C. squamosus	male	101.82	100.2	103.14	122	0.83

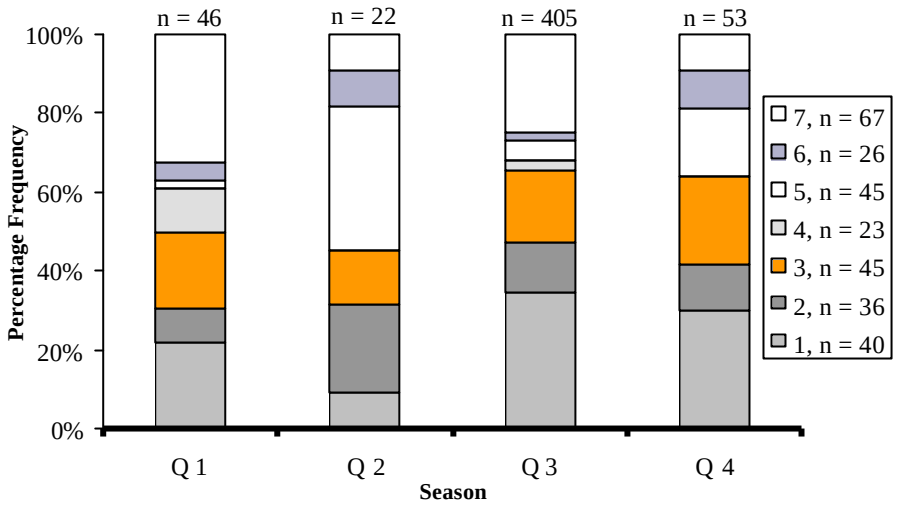


Fig. 3.40. Variation in frequency of occurrence of each maturity stage by quarter for *Centroscymnus coelolepis* females. Quarter refers to 3-month periods, December-February, March-May, June-August and September-November.

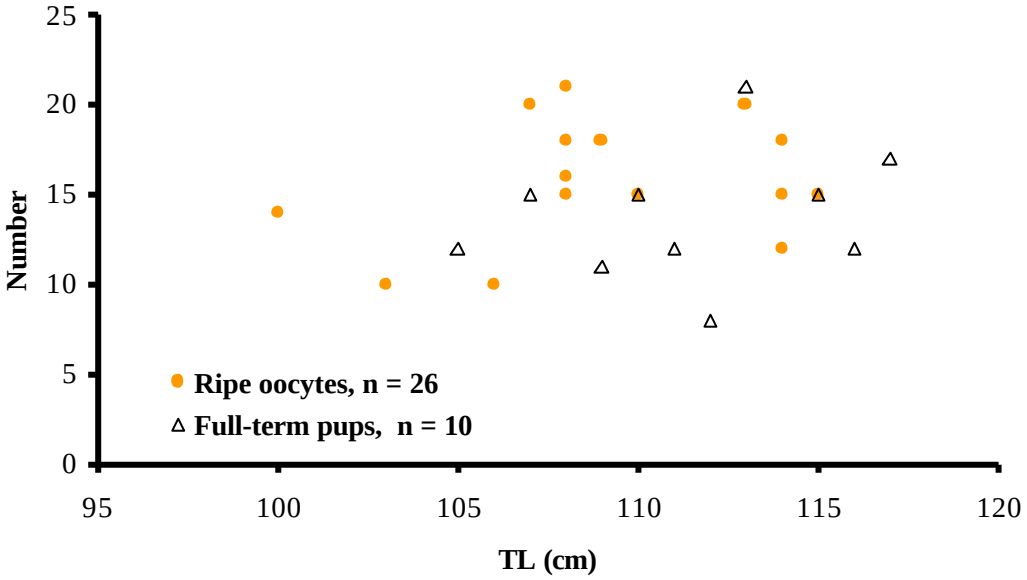


Fig. 3.41. Relationship between ovarian and uterine fecundity and TL of mature *Centroscymnus coelolepis*. In some cases only one uterus contained pups, probably due to stress-induced parturition.

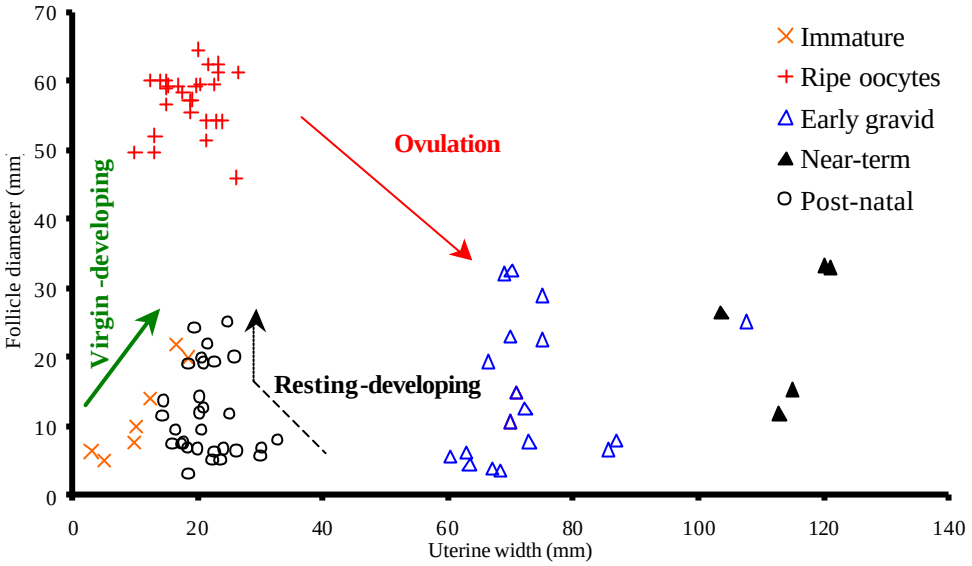


Fig. 3.42. Relationship between uterine width and diameter of largest ovarian follicle for *Centroscymnus coelolepis*. Ovaries of females that have already shed their pups begin to develop again

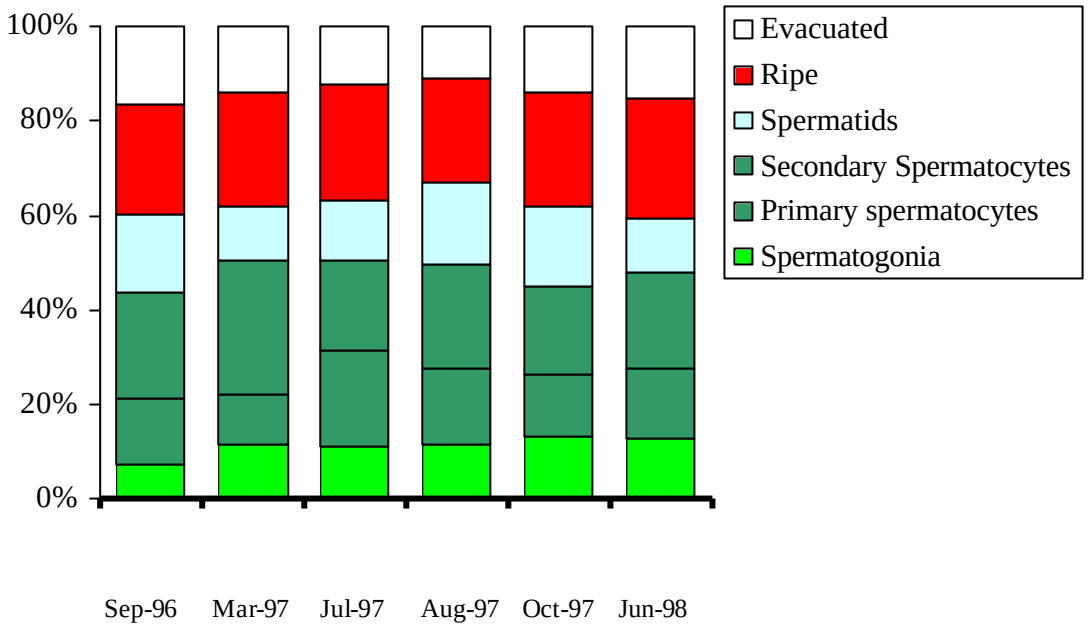


Fig. 3.43. Frequency of spermatocysts by sampled month containing each spermatogenic stage in *Centroscymnus coelolepis*.

Table 3.20. Counts of spermatocysts at each developmental stage from cross-sections of immature stage 2 *Centroscymnus coelolepis* testes, n = 4.

	Spermatogonia	Primary Spermatocyes	Secondary Spermatocytes	Spermatids	Ripe	Evacuated	Total
Mean	118	232	295	204	290	98	1120
S.D.	(88.7)	(107.3)	(95.5)	(41.1)	(42.3)	(33.3)	(244.9)

Table 3.21. Mean and 1 standard deviation of numbers of spermatocysts containing each stage of spermatogenic development for adult *Centroscymnus coelolepis* over the sampling period.

Month	Spermatogonia	Primary Spermatocytes	Secondary Spermatocytes	Spermatids	Ripe Spermatozoa	Evacuated	Total
September 1996	111	216	347	253	358	252	1621
n = 2	(8.5)	(60.8)	(11.3)	(19.8)	(30.4)	(99.7)	(37.9)
March 1997	146	135	355	146	304	177	1350
n = 3	(60.8)	(57.3)	(62.1)	(28.4)	(67.9)	(45.5)	(216.5)
July 1997	180	321	304	205	390	199	1688
n = 3	(129.5)	(74.5)	(82.7)	(37.6)	(163.6)	(16.6)	(21.2)
August 1997	248	336	466	376	462	236	2215
n = 2	(60.1)	(129.4)	(27.6)	(67.2)	(156.9)	(20.5)	(147.5)
October 1997	213	208	302	268	389	222	1690
n = 4	(76.5)	(61.7)	(94.5)	(91.1)	(125.3)	(57.7)	(138.4)
June 1998	229	259	360	202	451	274	1862
n = 3	(118.9)	(79.2)	(84.8)	(70.5)	(117.1)	(128.2)	(460.9)

3.2.4 Gonadosomatic and Hepatosomatic Index in *Centroscymnus coelolepis* and *Centrophorus squamosus*

As males of both species matured the Gonadosomatic Index (GSI) increased, as increasing resources were devoted to gonadal development. Fig. 3.44 and Table 3.22 show the change in GSI for *Centroscymnus coelolepis* and *Centrophorus squamosus* respectively. However there were differences in the process of development of the testes of these species. In *Centroscymnus coelolepis* (Fig. 3.45) the testes developed rapidly at first, but stage 2 and 3 specimens showed little further development in terms of width or weight. While sample sizes are low for *Centrophorus squamosus* (Fig. 3.46) it is clear that testes of stage 2 specimens undergo considerable development, and testes of stage 3 males were significantly wider than those of stage 2. Furthermore, the of degree of spermatogenesis in both species differed throughout the maturation process. The testes of all stages of *Centrophorus squamosus*, including immatures, contained ripe spermatozoa. In *Centroscymnus coelolepis*, immature (stage 1) testes contained no ripe spermatozoa. These differences are reflected in the relatively higher GSI for stage 1 males.

GSI data for females are contained in Table 3.22 and presented graphically in Fig. 3.47 and Fig. 3.48 for *Centroscymnus coelolepis* and *Centrophorus squamosus* respectively. It is clear that these species apportion differing amounts of resources to gonadal development. In *Centroscymnus coelolepis* ripe ova account for around 15 % of total body weight, while *Centrophorus squamosus*' ripe ovaries account for only half this percentage. Thus *Centroscymnus coelolepis* devotes twice the resources to gonadal development as *Centrophorus squamosus*. During the uterine stages the ovaries of *Centroscymnus coelolepis* become flaccid and account for a very small percentage of total weight. In *C. coelolepis*, no development of ovarian oocytes takes place during the phase of uterine development. This is in contrast to the shelf-dwelling squalids *Squalus acanthias* (Ford, 1921) and *Squalus japonicus* (Chen *et. al*. (1981) and the deepwater species *Centrophorus niaukang* (Yano and Kugai, 1993) and Centrophorus squamosus (Yano, *pers. comm*.).

Changes in Hepatosomatic Index (HSI) in *Centroscymnus coelolepis* and *Centrophorus squamosus* are presented in Table 3.23 and the change in HSI with maturity for male *Centroscymnus coelolepis* and *Centrophorus squamosus* are given in Fig. 3.49 and Fig. 3.50 respectively. Though sample size is smaller for *Centrophorus squamosus* there is little variation in liver weight as a percentage of total body weight at any stage of maturity. Data of HSI for females are shown in Fig. 3.51 and Fig. 3.52 respectively. Clearly *Centroscymnus coelolepis* of both sexes have relatively larger livers (up to 30 % of body weight) while the livers of *Centrophorus squamosus* are relatively smaller (about 20 % of body weight). The relationship between GSI and HSI in *Centroscymnus coelolepis* is interesting. As vitellogenesis proceeds in *Centroscymnus coelolepis* GSI increases to a peak in stage 3 fish, while HSI declines. This decline in HSI continued throughout gestation only recovering to pre-ovulatory levels after parturition. A similar relationship between GSI and HSI was demonstrated by Yano (1995) for *Centroscyllium fabricii*. For *Centrophorus squamosus* there was little evidence of declining HSI with vitellogenesis, and peak GSI corresponded to peak HSI. *Centroscymnus coelolepis* devotes twice the resources to gonadal development as does *Centrophorus squamosus*, but liver weight declines concomitantly. *Centrophorus squamosus* devotes less resources to gonadal development and does not display a decline in liver weight.

Table 3.22. Variation in GSI by maturity stage for male and female *Centrophorus squamosus* and *Centroscymnus coelolepis*.

Species	Sex	Mat	Mean	n	95 % C.I.	1 S.D.
C. coelolepis	Female	1	0.253	48	0.039	0.1384
		2	0.783	5		0.6189
		3	14.972	14	1.981	3.7827
		4	1.488	11	0.591	1.0009
		5	0.883	19	0.245	0.5440
		6	0.754	5		0.3476
		7	0.558	33	0.084	0.2473
C. coelolepis	Male	1	0.110	13	0.046	0.0849
		2	0.817	29	0.076	0.2080
		3	0.830	69	0.046	0.1960
C. squamosus	Male	1	0.275	3		0.1972
		2	0.241	6	0.096	0.1205
		3	0.400	22	0.035	0.0842
C. squamosus	Female	1	0.190	65	0.032	0.1330
		2	1.347	16	0.578	1.1797
		3	6.738	19	1.716	3.8169
		7	0.858	6	0.522	0.6527

Table 3.23. Variation in HSI by maturity stage for male and female *C. squamosus* and *C. coelolepis*

Species	Sex	Stage	Mean	95 % C.I.	n	1 S.D.
C. coelolepis	Male	1	31.591	4.544	22	10.8750
		2	31.550	2.370	24	5.9249
		3	30.214	0.728	84	3.4054
C. coelolepis	Female	1	30.439	2.999	43	10.0328
		2	28.535		2	4.6115
		3	21.737	1.807	15	3.5713
		4	19.020		3	6.1362
		5	18.876		3	6.5843
		7	22.016	1.798	22	4.3032
C. squamosus	Male	1	18.139		3	2.1796
		2	19.258		3	1.9193
		3	20.388	1.1958	15	2.3630
C. squamosus	Female	1	17.840	0.4857	29	1.3344
		2	18.937		4	2.2947
		3	20.649	1.0824	7	1.4611
		7	19.383		4	2.7466

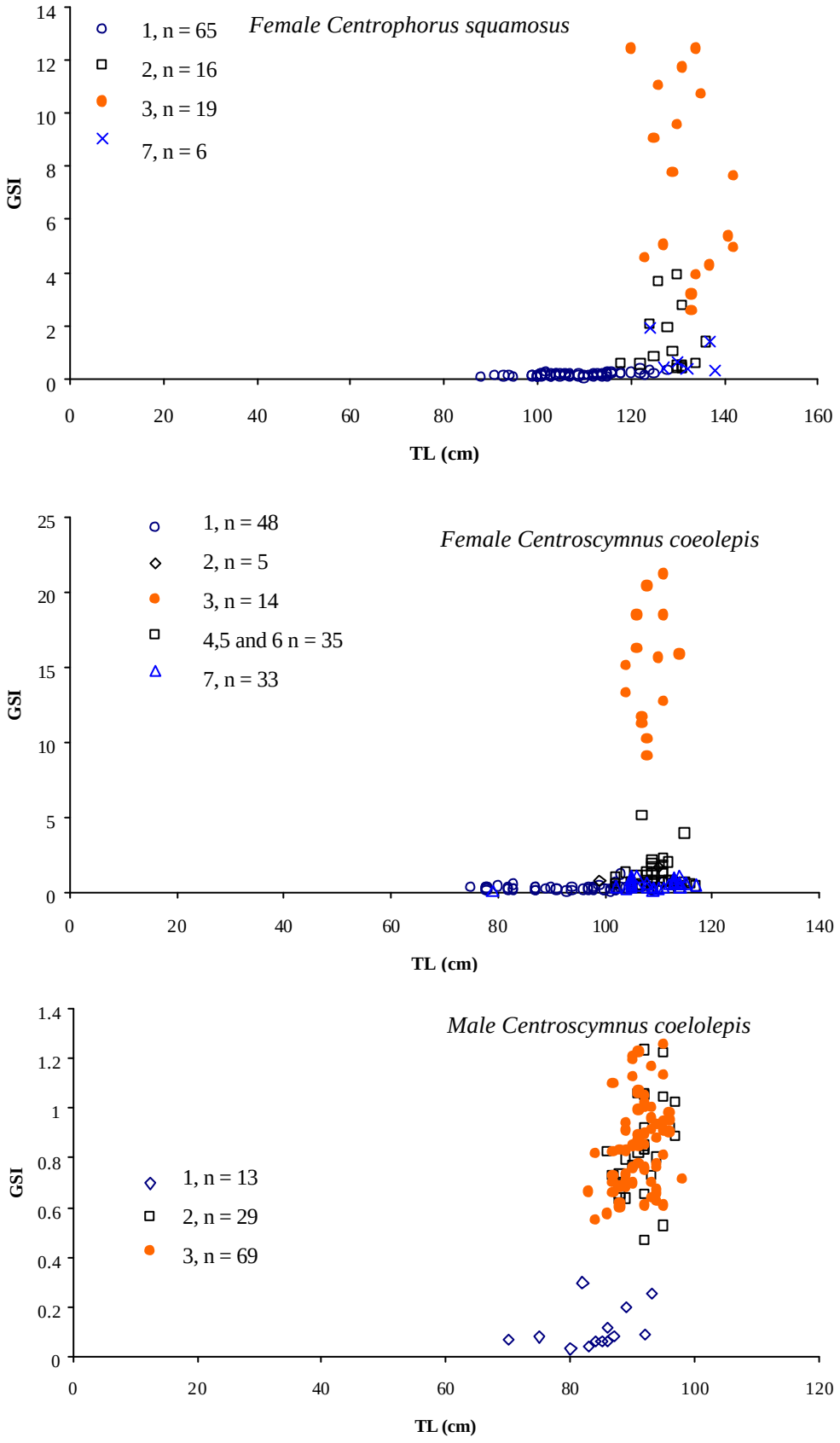


Fig. 3.44. Changes in GSI, based on round weights, with TL for C*entroscymnus coelolepis* and female *Centrophorus squamosus*.

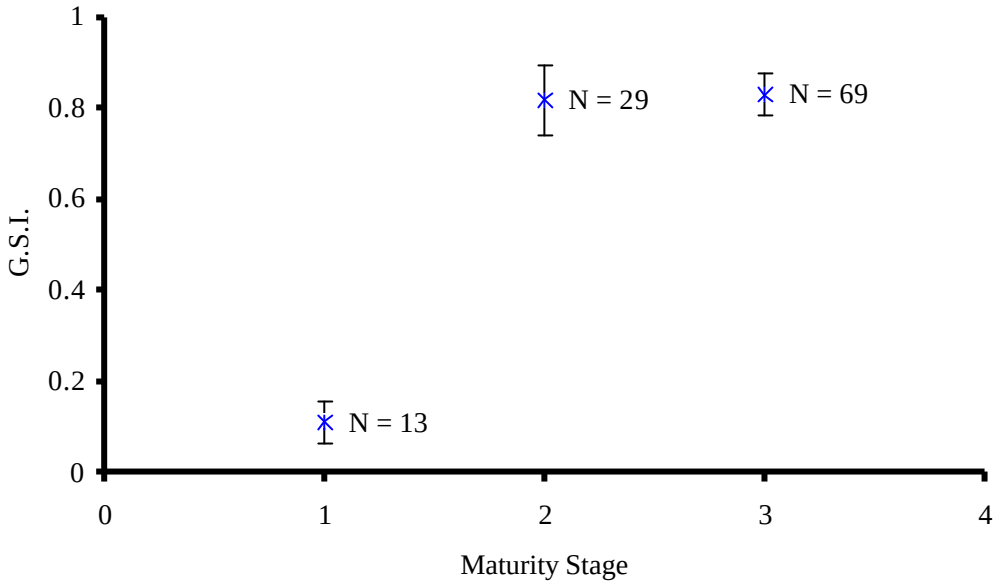


Fig. 3.45. Variation in Gonadosomatic index with 95 % confidence limits by stage of maturity in male *Centroscymnus coelolepis*.

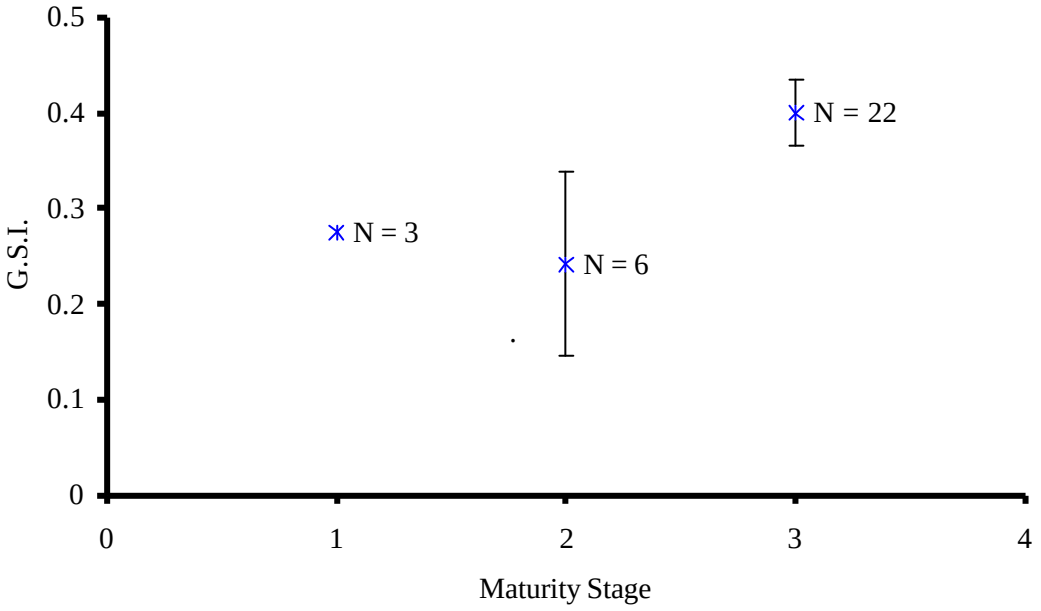


Fig. 3.46. Variation in Gonadosomatic Index (with 95 % confidence limits where n > 5) for male *Centrophorus squamosus*.

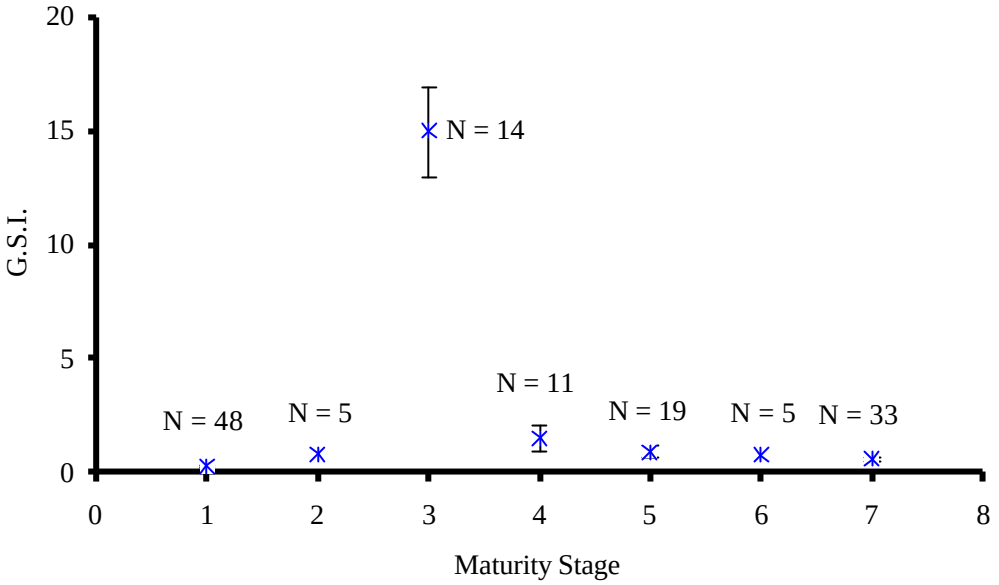


Fig. 3.47. Variation in Gonadosomatic Index (with 95 % confidence limits where N > 5) by maturity stage for female *Centroscymnus coelolepis*.

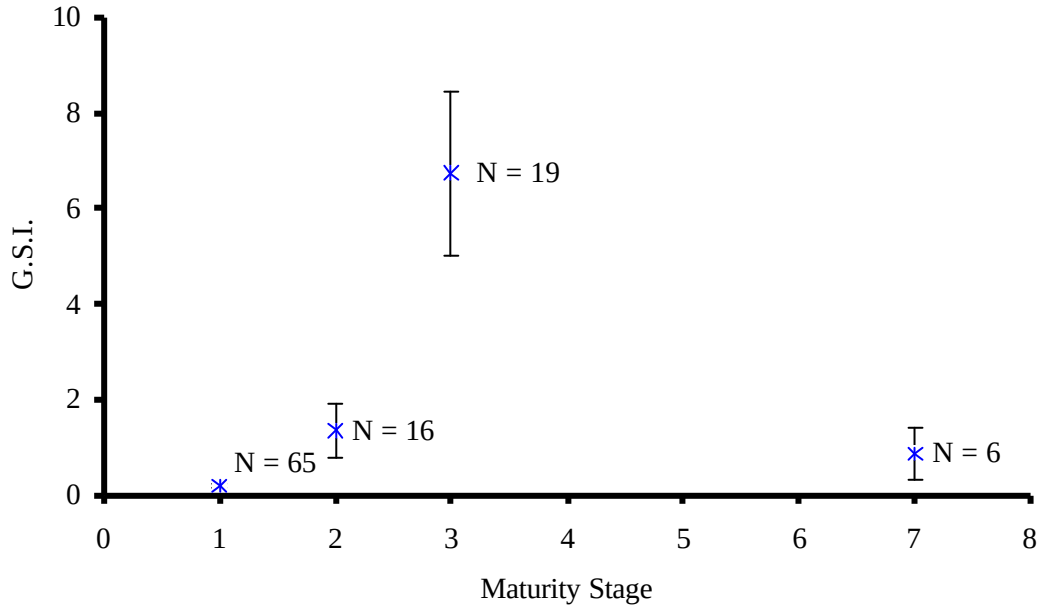


Fig. 3.48. Variation in Gonadosomatic Index (with 95 % confidence limits) by maturity stage for female *Centrophorus squamosus*.

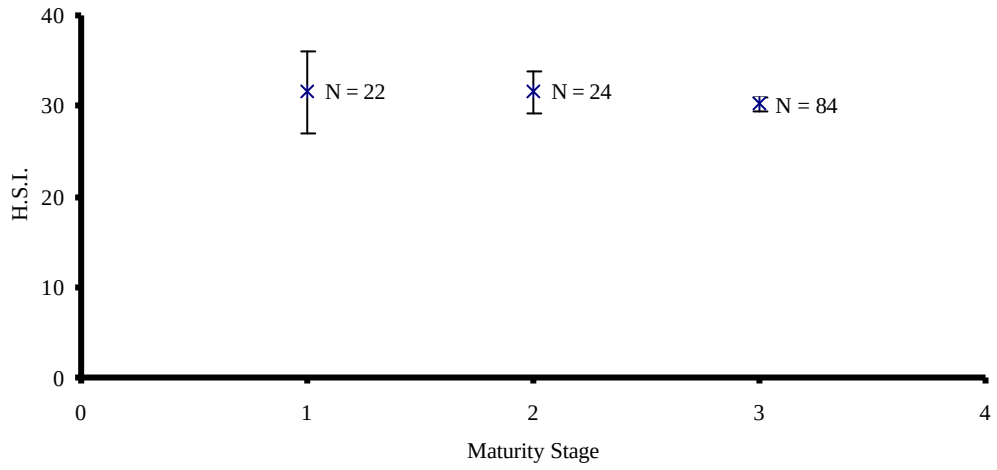


Fig. 3.49. Variation in Hepatosomatic Index (with 95 % confidence limits) by maturity stage for male *Centroscymnus coelolepis*.

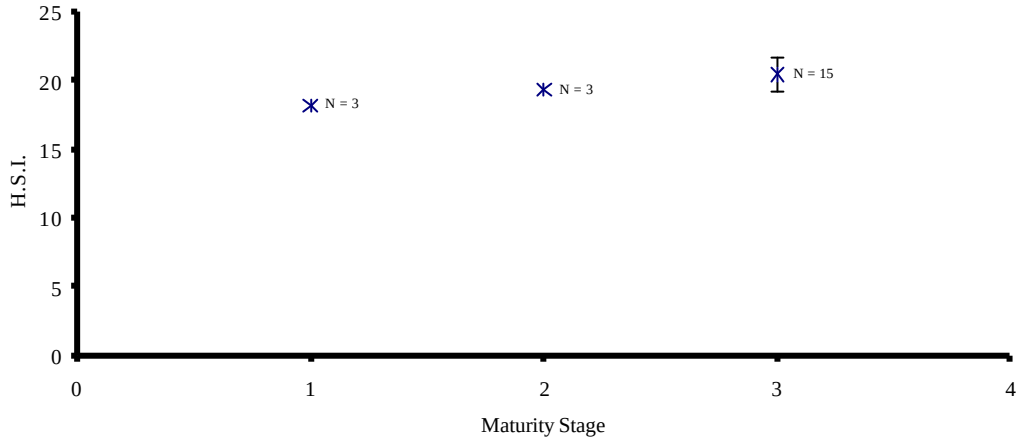


Fig. 3.50. Variation in Hepatosomatic Index (with 95 % confidence limits where N > 5) by maturity stage for male *Centrophorus squamosus*.

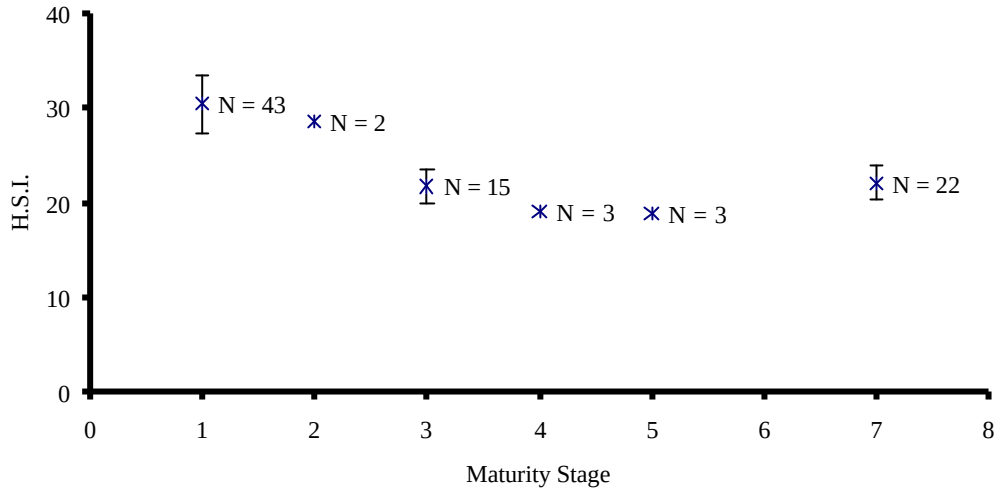


Fig. 3.51. Variation in Hepatosomatic Index (with 95 % confidence limits where n > 5) by maturity stage for female *Centroscymnus coelolepis*.

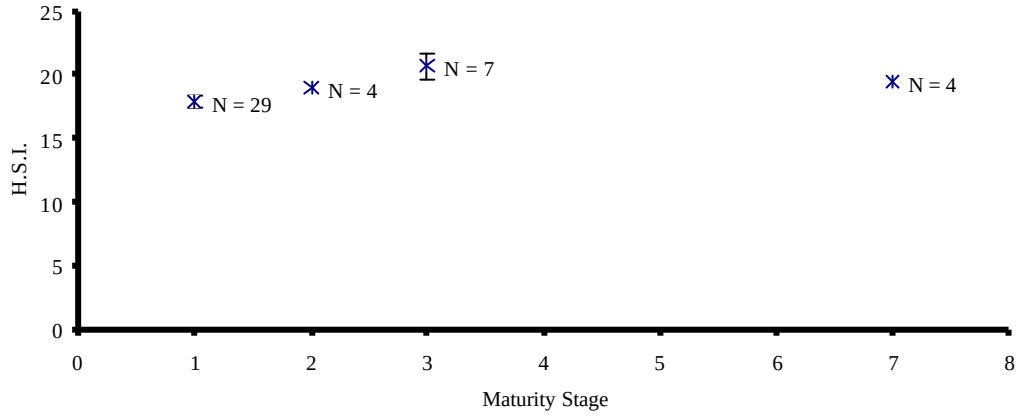


Fig. 3.52. Variation in Hepatosomatic Index (with 95 5 confidence limits where N > 5) by maturity stage for female *Centrophorus squamosus*.

3.2.5 Reproductive Cycle and Maturity of *Centrophorus squamous*

Stage 1 immature *Centrophorus squamosus* had small-undeveloped claspers and thread-like gonads. Plate 3.7 shows a stage 2 male. Males assigned to stage 2 and stage 3 had longer claspers, which were soft in stage 2 but became hard in stage 3. Testes in stages 2 and 3 *Centrophorus squamosus* were wider, and in stage 3 specimens they became somewhat convoluted. Fig. 3.33 shows the variation in testis width with increasing TL for maturity stages 2 and 3. The results of ANCOVA of testis width and TL at maturity stages 2 and 3 are contained in Table 3.15, while Table 3.16 summarises these results in anti-logarithmic scale. Mean width for stage 3 males was greater than for stage 2. Covariate (TL) by factor (testis width) interaction was not significant ($p > 0.2$) so ANCOVA was developed to test for significant differences in mean testis width adjusted for mean TL. Results of ANCOVA indicated that there was heterogeneity among adjusted mean testis width ($p < 0.01$). Therefore stage 3 testes were significantly wider than stage 2 testes.

Female *Centrophorus squamosus* assigned to stage 1 had whitish granular ovaries and thin thread-like uteri. Those assigned to stage 2 had widening uteri and ovaries containing vitellogenic eggs of various sizes. Fig. 3.53 shows the variation in uterus width with TL at each maturity stage. It is clear that uterine width increases with total length and that there is an abrupt increase in width between stages 1 and 2. There was some difficulty in deciding whether some individuals should be assigned to stage 2 or 7. In these cases the uteri were wide and the ovaries contained some oocytes in various stages of development and aspherical, yellow degenerate follicles. Inspection of the inside of the uteri of these fish showed a degree of villification, similar to that observed in post-natal *Centroscymnus coelolepis*. Individuals with more flaccid uteri and ovaries that contained degenerate follicles were assigned to stage 7. There was no significant difference in widths of left and right uteri for all maturity stages combined (t-test, $p > 0.4$) therefore uteri data were combined before further analysis. Width data for stage 1 females were removed from the analysis because they were not in the same range of either variable. Table 3.15 contains the mean uterus width data in logarithmic form. Table 3.17 contains the results of uterus width as compared by Gabriel's approximate method, these results are also presented graphically in Fig. 3.37. There was some evidence that the covariate (TL) by factor

(maturity stage) interaction was significant ($p = 0.06$). Therefore Gabriel's approximate method was used to test for significant differences in the uterus width-TL regression coefficients. The regression coefficient for stage 2 uterus width on TL was significantly different from the other two stages. Gabriel's approximate method did not detect significant differences in regression coefficients between stages 3 and 7. Therefore ANCOVA was developed to test for a significant difference in mean uterus width at adjusted mean TL between these two stages. ANCOVA showed that there was evidence of a significant difference ($p < 0.05$) in mean uterus width. This indicated that uterus widths were significantly different between the two stages. The greater mean width for stage 7 uteri suggested that the fish assigned to stage 7 had indeed already carried embryos, and may have given birth quite recently. The regression coefficient for stage 2 uteri indicates negative allometry, the uteri growing smaller with increasing TL. Thus the uteri of females considered to be "ripening" tended to grow smaller in larger females, and the mean rate of change in their width with increasing TL was significantly different from that of uteri of stage 3 or 7 females. This indicates a recrudescence of uteri and suggests that a portion, at least, of females assigned to stage 2 had already carried pups also. While it is not clear what proportion of stage 2 females had already given birth these findings suggest a prolonged resting phase after parturition.

While the maturity scale was insufficient for the purposes of determining whether a given female had already given birth, it was sufficient for the purposes of assessing functional maturity in the population. The numbers and proportions mature at each successive length class are presented in Table 3.24 for females and in Table 3.25 for males while the results of Probit analysis are contained in Table 3.19. In general increased proportions of mature fish accompanied each successive length increment in males and females. Probit analysis yielded TL_{50} estimates of 101.82 cm for males and 126.24 cm for females. The results of Probit analysis of proportions mature are given in Fig. 3.54 for females and Fig. 3.55 for males. This species reaches sexual maturity at very large size, 84 % of male and 88 % of female TL. Maturity is reached at largest size as a proportion of TL for any of the species under study. Length frequency data for trawl and long-line (Section 3.1.6) indicate that large proportions of mature males, though very few females present in the catches fom either gear type were larger than

size at 50 % maturity. Fishing in the study area will have little or no impact on the gravid of the *Centrophorus squamosus*.

The relative frequencies of each maturity stage by month are shown in Fig. 3.56. Only 4 stages of female maturity were recorded during this study. However, each of these stages occurred in each of the months sampled. The relative frequencies varied. However no seasonal maximum frequency of females with ripe ova or post-natal females was observed. Some months (March and December 1997) had relatively more stage 3 individuals. Despite the lack of samples from all seasons of the year it does not appear that a seasonal cycle of reproductive activity exists in female *Centrophorus squamosus*.

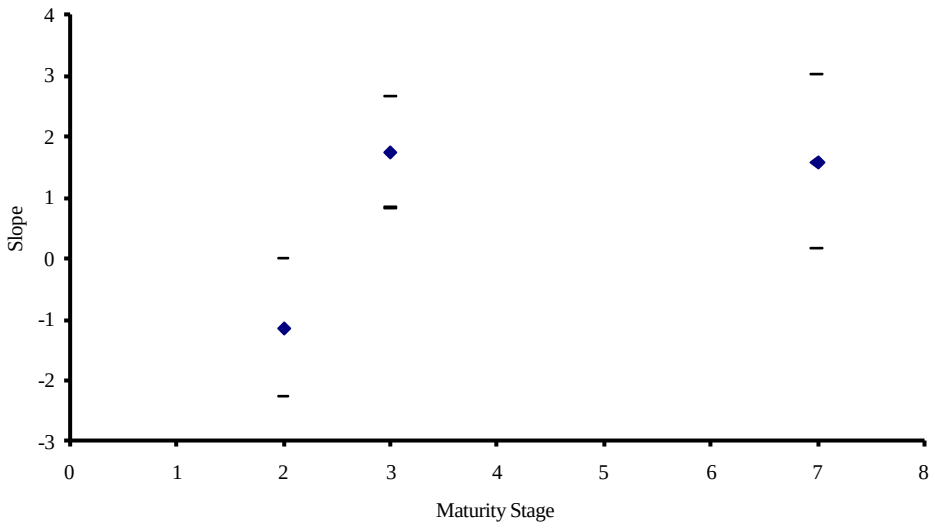


Fig. 3.53. Comparisons of regression coefficient (slope) of allometric function of uterus width on total length for *C. squamosus* using Gabriel's approximate method.

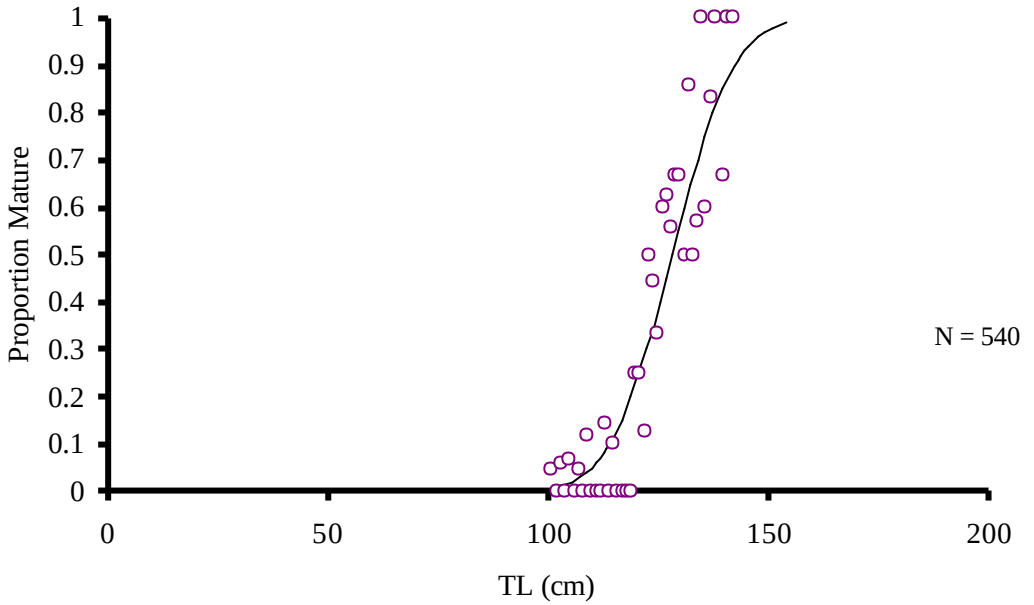


Fig. 3.54. Maturity ogive for female *Centrophorus squamosus* fitted by probit analysis. Total length at 50 % maturity in the sampled population 128 cm.

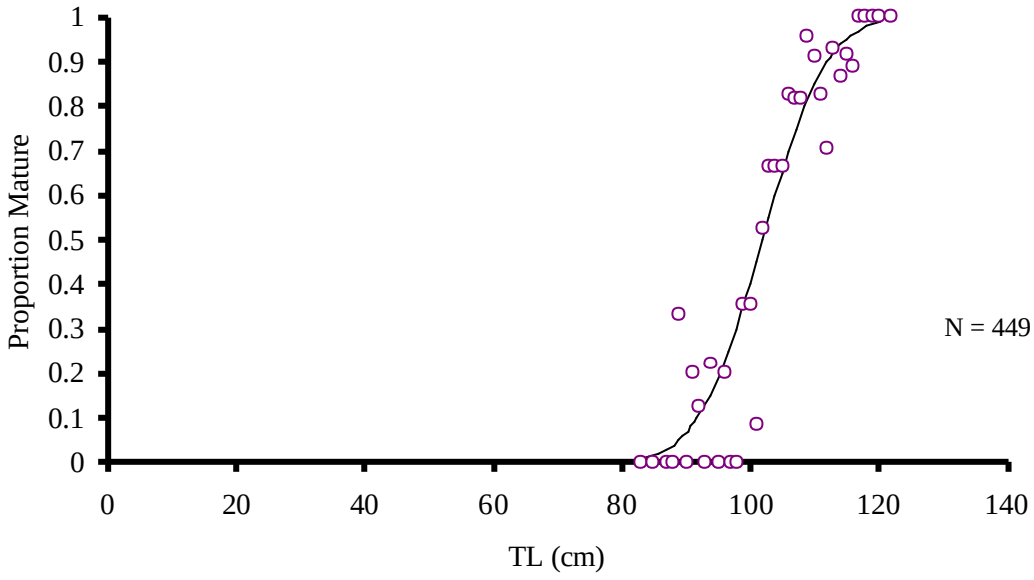


Fig. 3.55. Maturity ogive for male *Centrophorus squamosus* fitted by probit analysis. Total length at 50 % maturity in the sampled population 102 cm.

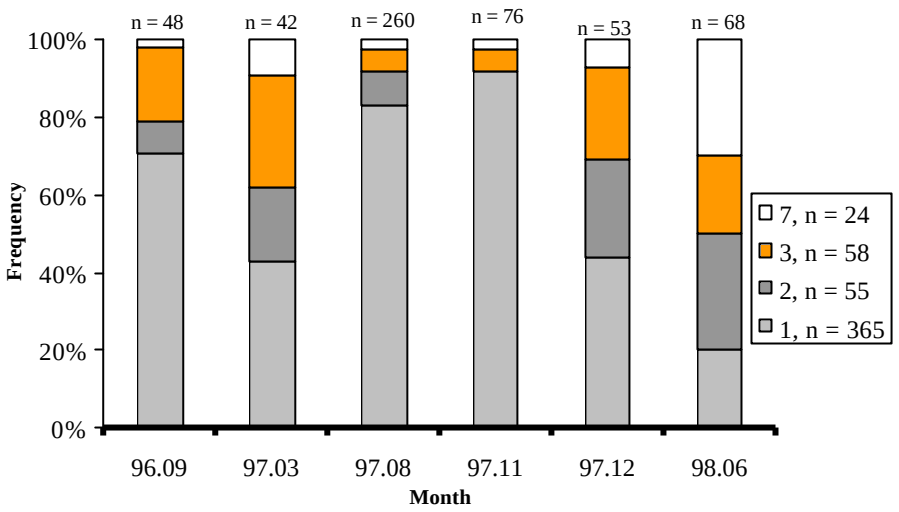


Fig. 3.56. Variation in frequency of occurrence of each maturity stage by quarter for *Centrophorus squamosus* females.

Table 3.24. Numbers and proportions mature by length increment for female *Centrophorus squamosus.*

TL (cm)	Total No.	No. Mature	Proportion Mature	TL (cm)	Total No.	No. Mature	Proportion Mature
77	1	0	0.00	111	9	0	0.00
85	3	0	0.00	112	22	0	0.00
86	1	0	0.00	113	7	1	0.14
87	1	0	0.00	114	10	0	0.00
88	3	0	0.00	115	10	1	0.10
89	1	0	0.00	116	7	0	0.00
90	4	0	0.00	117	5	0	0.00
91	7	0	0.00	118	6	0	0.00
92	4	0	0.00	119	2	0	0.00
93	7	0	0.00	120	4	1	0.25
94	7	0	0.00	121	4	1	0.25
95	14	0	0.00	122	8	1	0.13
96	18	0	0.00	123	8	4	0.50
97	21	0	0.00	124	9	4	0.44
98	16	0	0.00	125	9	3	0.33
99	13	0	0.00	126	10	6	0.60
100	20	0	0.00	127	8	5	0.63
101	22	1	0.05	128	9	5	0.56
102	21	0	0.00	129	6	4	0.67
103	17	1	0.06	130	12	8	0.67
104	22	0	0.00	131	10	5	0.50
105	15	1	0.07	132	7	6	0.86
106	21	0	0.00	133	8	4	0.50
107	21	1	0.05	134	7	4	0.57
108	10	0	0.00	135	3	3	1.00
109	17	2	0.12	136	5	3	0.60
110	12	0	0.00	137	6	5	0.83
				138	2	2	1.00
				140	3	2	0.67
				141	2	2	1.00
				142	2	2	1.00

Table 3.25. Numbers and proportions mature by length increment for male *Centrophorus squamosus.*

TL (cm)	Total No.	No. Mature	Proportion Mature	TL (cm)	Total No.	No. Mature	Proportion Mature
83	1	0	0.00	105	21	14	0.67
85	1	0	0.00	106	35	29	0.83
87	1	0	0.00	107	33	27	0.82
88	2	0	0.00	108	33	27	0.82
89	6	2	0.33	109	23	22	0.96
90	4	0	0.00	110	23	21	0.91
91	5	1	0.20	111	29	24	0.83
92	8	1	0.13	112	17	12	0.71
93	3	0	0.00	113	14	13	0.93
94	9	2	0.22	114	15	13	0.87
95	5	0	0.00	115	12	11	0.92
96	10	2	0.20	116	9	8	0.89
97	9	0	0.00	117	6	6	1.00
98	6	0	0.00	118	7	7	1.00
99	17	6	0.35	119	2	2	1.00
100	17	6	0.35	120	1	1	1.00
101	12	1	0.08	122	1	1	1.00
102	19	10	0.53				
103	15	10	0.67				
104	18	12	0.67				

3.2.6 Fecundity of *Centrophorus squamosus*

The relationship between ovarian fecundity and TL is shown in Fig. 3.57. No gravid females were recorded in this study so the only fecundity information available related to counts from the ovaries that ranged from 6 to 11 (mean = 8) ripe oocytes per female. As with *Centroscymnus coelolepis* there was little increase in fecundity with TL, but some larger females had higher oocyte counts.

3.2.7 Spermatogenesis in *Centrophorus squamosus*

Mean number of spermatocysts containing spermatozoa at each stage of maturation are presented in Table 3.26 for immature stage 1 and 2 testes, Table 3.27 shows the mean numbers for mature (stage 3) male. Testes of stage 1 and 2 (immature and ripening) *Centrophorus squamosus* contained all stages of spermatogenic activity. However, the numbers of ripe and evacuated spermatocysts was small in relation to mature fish.

The relative frequencies of each spermatogenic stage by month sampled are presented in Fig. 3.58. All stages of spermatogenesis were present in the testes from all months sampled. There was no apparent change in the frequency of any stage of spermatogenesis across the sampling period. Spermatocysts containing ripe spermatozoa were the most numerous stage in all months. There was no significant difference in mean counts of ripe or evacuated spermatocysts between sampled months (ANOVA, $p > 0.5$) with the relative proportions of each stage much the same throughout. This suggests that that there is no seasonal cycle in the testis of this species. However samples were not available for all months of the year and the evidence is not as strong as for *Centroscymnus coelolepis*.

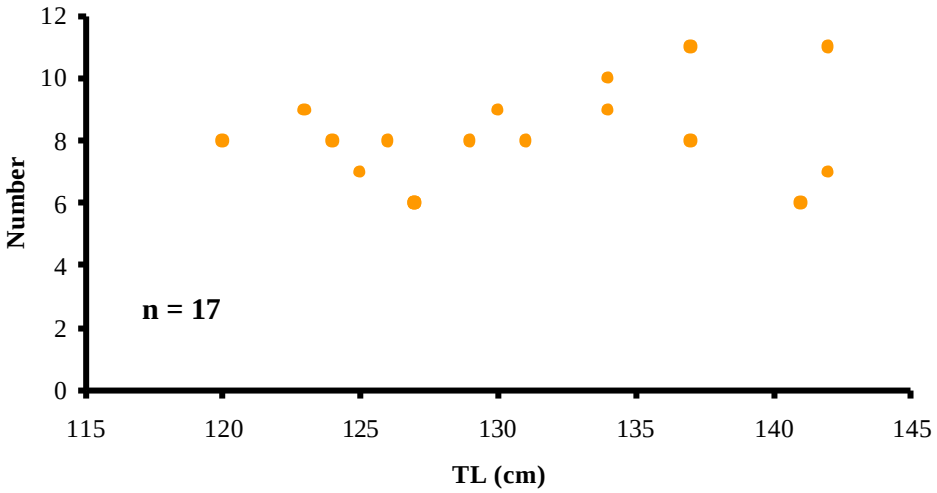


Fig. 3.57. Relationship between ovarian fecundity and TL of mature *Centrophorus squamosus*.

Table 3.26. Counts of spermatocysts at each developmental stage from cross-sections of immature stage I and II *Centrophorus squamosus* testes. Mean and standard deviation (S.D.) given for stage II.

Stage	Spermatogonia	Primary Spermatocytes	Secondary Spermatocytes	Spermatids	Ripe	Evacuated	Total
1	104	135	76	51	64	27	443
n = 2	(24.0)	(27.6)	(32.5)	(7.8)	(56.6)		(9.2)
2	106	225	139	138	148	52	808
n = 6	(24.6)	(28.5)	(34.3)	(49.6)	(44.2)	(40.8)	(192.8)

Table 3.27. Mean and standard deviation of counts of spermatocysts containing each stage of spermatogenesis from cross-sections mature *Centrophorus squamosus* testes.

Month	Spermatogonia	Primary Spermatocyte	Secondary Spermatocyte	Spermatid	Ripe	Evacuated	Total
Sep-96	273	428.5	403	358.5	455	479	2397
n = 2	(179.6)	(181.7)	(271.5)	(36.1)	(100.4)	(357.8)	(220.6)
Aug-97	118	211	262	240	377	241	1368
n = 3	(14.5)	(22.3)	(61.9)	(53.6)	(69.2)	(98.3)	(215.4)
Oct-97	82	184	234	193	429	295	1415
n = 2	(3.5)	(0.7)	(29.7)	(137.9)	(19.8)	(120.9)	(244.7)
Nov-97	88	194	230	288	336	187	1323
n = 3	(18.0)	(112.0)	(116.1)	(139.8)	(136.3)	(79.0)	(376.9)

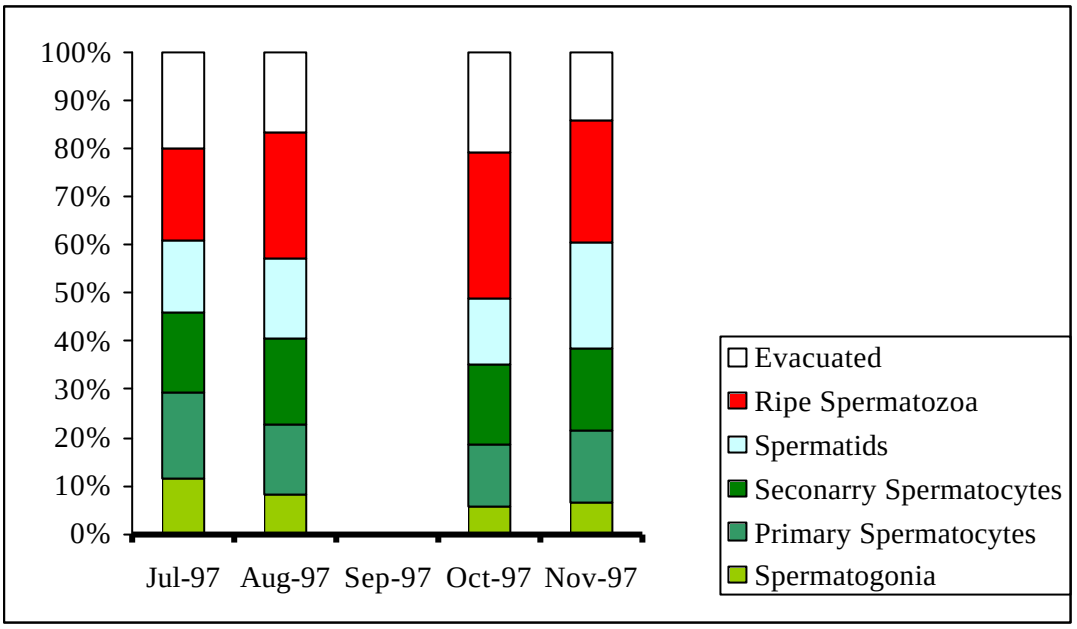


Fig. 3.58. Frequency of spermatocysts by sampled month of spermatocysts containing each spermatogenic stage in *Centrophorus squamosus*.

Fec sq

Table 3.26. Counts of spermatocysts at each developmental stage from cross-sections of immature stage I and II *Centrophorus squamosus* testes. Mean and standard deviation (S.D.) given for stage II.

Stage	Spermatogonia	Primary Spermatocytes	Secondary Spermatocytes	Spermatids	Ripe	Evacuated	Total
1	104	135	76	51	64	27	443
n = 2	(24.0)	(27.6)	(32.5)	(7.8)	(56.6)		(9.2)
2	106	225	139	138	148	52	808
n = 6	(24.6)	(28.5)	(34.3)	(49.6)	(44.2)	(40.8)	(192.8)

Table 3.27. Mean and standard deviation of counts of spermatocysts containing each stage of spermatogenesis from cross-sections mature *Centrophorus squamosus* testes.

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n = 2	(179.6)	(181.7)	(271.5)	(36.1)	(100.4)	(357.8)	(220.6)
Aug-97	118	211	262	240	377	241	1368
n = 3	(14.5)	(22.3)	(61.9)	(53.6)	(69.2)	(98.3)	(215.4)
Oct-97	82	184	234	193	429	295	1415
n = 2	(3.5)	(0.7)	(29.7)	(137.9)	(19.8)	(120.9)	(244.7)
Nov-97	88	194	230	288	336	187	1323
n = 3	(18.0)	(112.0)	(116.1)	(139.8)	(136.3)	(79.0)	(376.9)

Sperm graph sq

3.2.8 Reproductive cycle and maturity in *Deania calceus*

Gravid and post-natal females were only found in December 1999, on the slopes of the Porcupine Bank (survey areas 5 to 8, Fig. 2.1). The gravid females were taken from depths of 500 to 1,100 m and near-term females from 500 to 800 m depth. Comprehensive information on maturity was only available for a few months. The variation in frequency of maturity stages by month is shown in Fig. 3.61. The inventory of maturity information was more limited for *Deania calceus* than for the other species. Therefore it was not possible to determine if there was a defined breeding season.

Stage 1 males had tiny claspers and threadlike testes, while those assigned to stage 2 had soft, though long claspers and wider testes. The sperm ducts were straight in stage 1 but slightly coiled in stage 2. Stage 3 males had hard claspers and the testes were fully developed and the sperm ducts were tightly coiled. Females assigned to stage 1 had narrow uteri and whitish almost transparent ovaries. Stages 2 and 3 had wider uteri. The oocytes reached a maximum diameter of 41 mm.

The numbers and proportions of mature males and females for each successive length class are given in Table 3.28 and Table 3.29 respectively, while the results of Probit analysis are contained in Table 3.18. The Probit analyses are presented in Fig. 3.59 for males and Fig. 3.60 for females. In both sexes there was an overall tendency for successive increases in the proportions mature with increasing length. The largest specimens of both sexes exhibited 100 % maturity. Probit analysis yielded results TL_{50} estimates of 85.16 cm for males and 105.03 cm for females. The larger value for females agrees with the greater lengths attained. Estimates of length at 50 % maturity of *Deania calceus* are the first for that species and indicate that it attains sexual maturity only at large size. As for the other species, males mature at a smaller proportion of maximum length (78 %) as opposed to females (86 %). The size selectivity of the fishing gear has important implications for *Deania calceus*. Large females are able to avoid trawls but are caught on long-line (Section 3.1.4). Furthermore modal length of long-line caught females corresponds to size at 50 % maturity, indicating that the "spawning stock" of this species will be especially vulnerable to long-line fishing.

3.2.9 Fecundity of *Deania calceus*

Only a small number of female *Deania calceus* in the final stages of ovarian (stage 3) or uterine (stage 6) development were recorded. However counts of ripe ovarian oocytes ranged from 6 to 14 per female (mean 13). Only two stage 6 females were secured in this study. Counts of near-term pups from these specimens yielded counts of 8 and 14 each. Mean TL of pups was 17.6 cm and 22.6 cm for the stage 6 females.

3.2.10 Spermatogenesis in *Deania calceus*

The mean number of spermatocysts at each stage of spermatogenesis are given for stage 1 and 2 immature males in Table 3.30, while the mean number for mature, stage 3, specimens is given in Table 3.31. Testes from both stage 1 and stage 2 immature males contained all stages of spermatogenesis the numbers of ripe and evacuated spermatocysts were small by comparison with mature testes. All stages of spermatogenesis were present in testes of mature males throughout the sampling period for this species. The frequency of each spermatogenic stage by month for mature males is shown in Fig. 3.62. There was no evidence of change in the frequency of any stage by month. There was no significant difference in mean counts of ripe spermatocysts across the sampling period (ANOVA, $p > 0.4$).

Table 3.28. Numbers and proportions mature by length increment for male *Deania calceus*.

TL (cm)	Total No.	No. Mature	Proportion Mature	TL (cm)	Total No.	No. Mature	Proportion Mature
58	1	0	0.00	79	28	9	0.32
62	1	0	0.00	80	45	16	0.36
63	1	0	0.00	81	47	18	0.38
64	2	0	0.00	82	60	25	0.42
65	1	0	0.00	83	58	36	0.62
66	2	0	0.00	84	95	54	0.57
67	1	0	0.00	85	88	44	0.50
68	4	0	0.00	86	89	44	0.49
69	5	0	0.00	87	68	35	0.51
70	2	0	0.00	88	49	20	0.41
71	1	0	0.00	89	39	30	0.77
72	6	0	0.00	90	15	7	0.47
73	7	0	0.00	91	12	5	0.42
74	10	1	0.10	92	10	9	0.90
75	9	0	0.00	94	3	3	1.00
76	12	1	0.08	97	1	1	1.00
77	19	0	0.00	98	1	1	1.00
78	19	4	0.21				

Table 3.29. Numbers and proportions mature by length increment for female *Deania calceus*.

TL (cm)	Total No.	No. Mature	Proportion Mature	TL (cm)	Total No.	No. Mature	Proportion Mature
52	1	0	0.00	86	30	0	0.00
56	1	0	0.00	87	16	2	0.13
57	1	0	0.00	88	15	0	0.00
59	1	0	0.00	89	18	0	0.00
60	1	0	0.00	90	16	0	0.00
61	1	0	0.00	91	16	2	0.13
62	3	0	0.00	92	21	1	0.05
63	2	0	0.00	93	7	0	0.00
66	3	0	0.00	94	13	0	0.00
67	5	0	0.00	95	9	1	0.11
68	2	0	0.00	96	10	2	0.20
69	3	0	0.00	97	12	0	0.00
70	5	0	0.00	98	12	3	0.25
71	5	0	0.00	99	7	3	0.43
72	6	0	0.00	100	17	9	0.53
73	8	1	0.13	101	13	6	0.46
74	9	1	0.11	102	17	8	0.47
75	6	0	0.00	103	15	10	0.67
76	6	0	0.00	104	9	3	0.33
77	10	0	0.00	105	13	7	0.54
78	12	0	0.00	106	8	2	0.25
79	7	0	0.00	107	5	3	0.60
80	11	0	0.00	108	2	1	0.50
81	27	1	0.04	109	6	5	0.83
82	24	2	0.08	111	2	2	1.00
83	18	1	0.06	112	2	2	1.00
84	25	2	0.08	116	1	1	1.00
85	28	3	0.11				

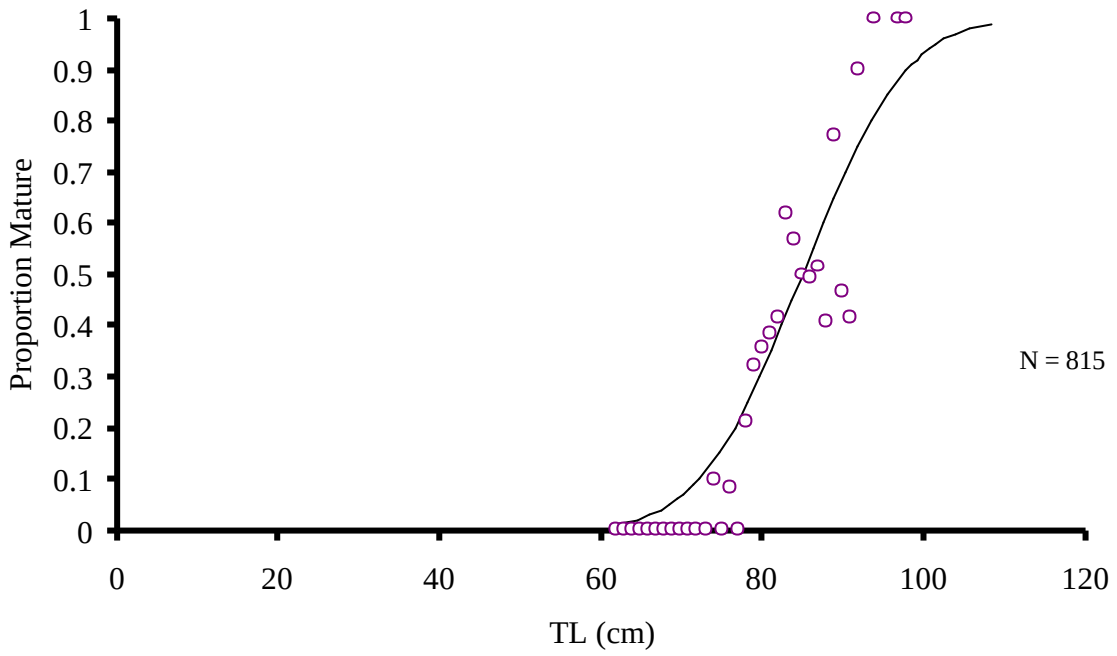

Fig. 3.59. Maturity ogive for male *Deania calcea* fitted by probit analysis. TL at 50 % maturity in sampled population 85 cm.

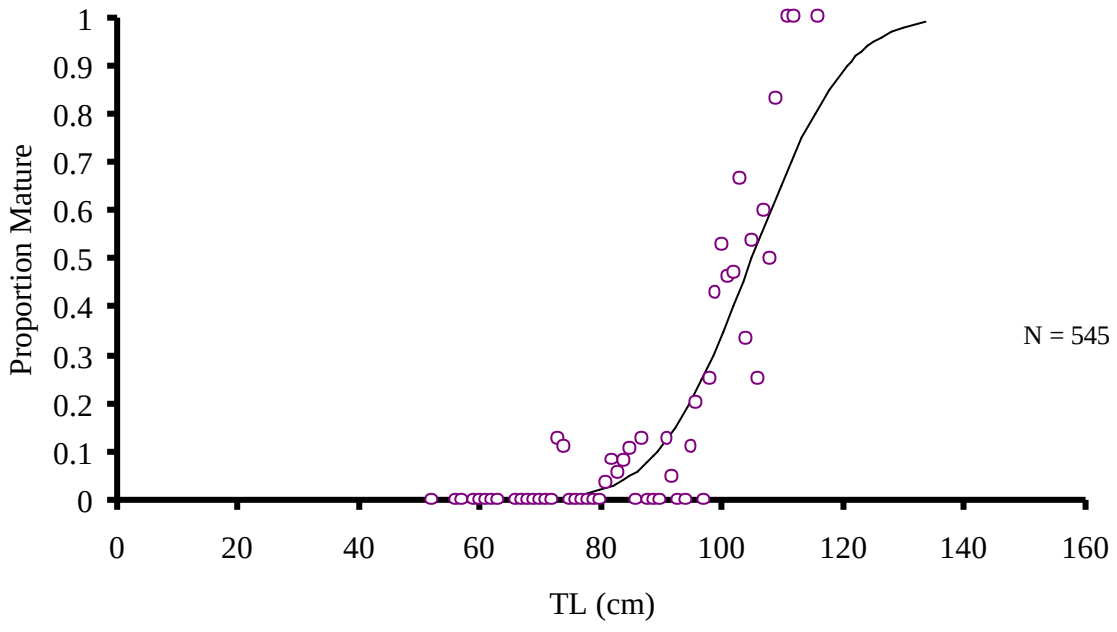

Fig. 3.60. Maturity ogive for female *Deania calcea* fitted by probit analysis. TL at 50 % maturity in sampled population 105 cm.

Table 3.30. Counts of spermatocysts at each developmental stage from cross-sections of immature stage 1 and 2*Deania calceus* testes. Mean and standard deviation (S.D.) given for stage 2.

Stage	Spermatogonia	Primary Spermatocytes	Secondary Spermatocytes	Spermatids	Ripe	Evacuated	Total
1	60	105	109	93	127	34	529
n = 2	(24.0)	(19.8)	(24)	(64.3)	(24.7)	(31.1)	(140)
2	83	202.25	258.5	267.5	288.5	60.5	1160.25
n = 4	(59.4)	(57.7)	(92.9)	(142.6)	(43.4)	(35.8)	(331.1)

Table 3.31. Mean and standard deviation of counts, where n > 1, of spermatocysts containing each stage of spermatogenesis from cross-sections mature Deania calcea testes.

Month	Spermatogonia	Primary Spermatocyes	Secondary Spermatocytes	Spermatids	Ripe	Evacuated	Total
Sep-96	127	218	174	190	210	177	1096
n = 1							
Aug-97	159	181	429	230	420	277	1694
n = 2	(45.3)	(68.6)	(129.4)	(77.1)	(104.7)	(48.8)	(124.5)
Oct-97	198	195	272	192	310	265	1430
n = 2	(70)	(10.6)	(238.3)	(12.7)	(67.2)	(265.9)	(26.9)
Nov-97	147	239	275	277	298	281	1517
n = 8	(72)	(77.5)	(108.8)	(170.1)	(114.5)	(128.5)	(493.2)
Dec-97	112	180	215	228	292	220	1246
n = 6	(34.9)	(20.9)	(47.8)	(68.6)	(60.7)	(39.8)	(181.4)

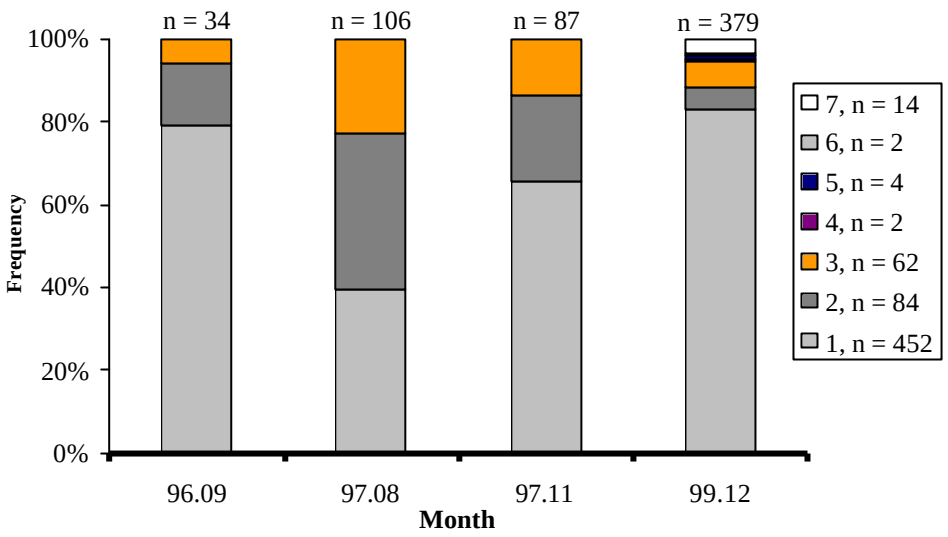

Fig. 3.61. Variation in frequency of occurrence of each maturity stage by quarter for *Deania calceus* females.

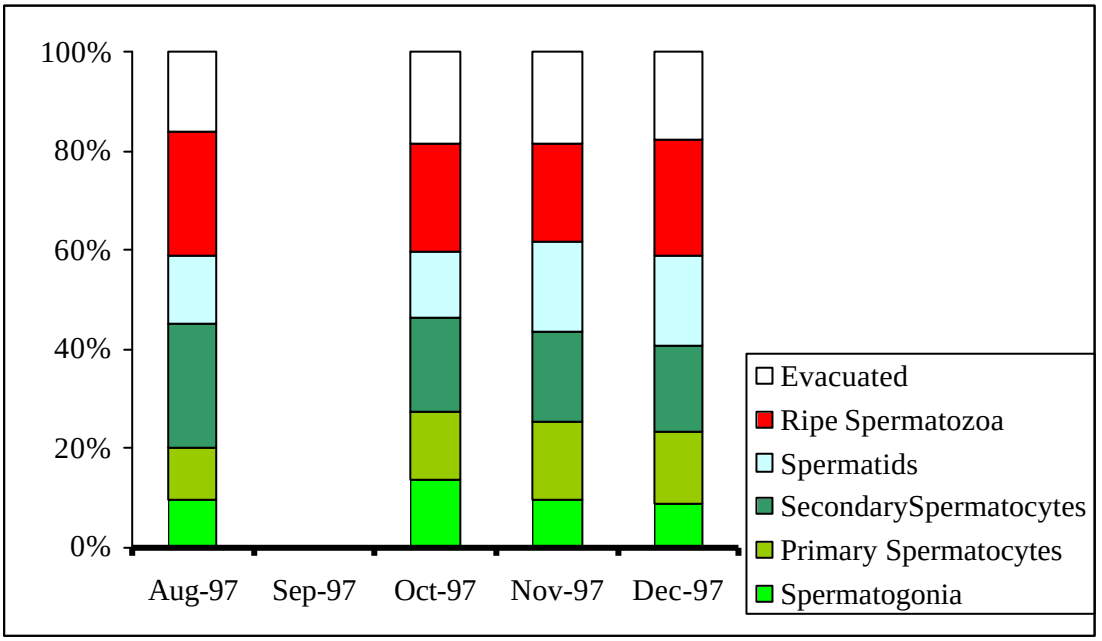

Fig. 3.62. Frequency of spermatocysts by sampled month of spermatocysts containing each spermatogenic stage in *Deania calceus.*

3.2.11 Testicular structure and spermatogenesis

In all species under study the testes were paired structures suspended from the dorsal wall of the peritoneal cavity by the mesorchia. In cross-section it was shown that the testes were composed of spherical ampullae containing spermatogenic cells, each ampulla containing cells in the same stage of spermatogenesis. These spherical structures are here referred to as spermatocysts after Grier (1992). The germinal ridge, which runs the entire length of the testis was located along the ventro-lateral face of the organ. Spermatocysts representing successive stages of spermatogenesis formed concentric zones radiating from the germinal ridge proximally. This organisation of the testis conforms to the "diametric type" as described by Pratt (1988).

The organisation and structure of spermatogenesis was largely the same for each of the three species under study and is described in detail for *Deania calceus*. The descriptions of the testicular structure of *Deania calceus* are the first for this species. The various stages of spermatogenesis are shown in Plates 3.8 to 3.12 for *Deania calceus*, in Plates 3.13 to 3.18 for *Centroscymnus coelolepis* and in Plates 3.19 to 3.23 for *Centrophorus squamosus*. Histological plates of *Deania calceus* are used to illustrate the important features of maturation of spermatozoa. Spermatocysts containing primary spermatogonia were found in the germinal region of the testis. As in all stages of spermatogenesis the spermatocysts were easily identified by the basement membrane. The spherical nuclei of the spermatogonia were arranged around the basement membrane while the Sertoli cells (elliptical) were arrayed around the lumen of spermatocysts (Plate 3.8). In spermatocysts containing secondary spermatogonia the Sertoli cells began to move towards the basement membrane. Spermatocysts containing primary spermatocytes (Plate 3.9) were characterised, in all species, by granular, basophilic nuclei and Sertoli cells arranged along the basement membrane Primary spermatocytes undergo the first meiotic division to become secondary spermatocytes. Secondary spermatocytes' nuclei were characteristically small and denser staining than those of the primary spermatocytes which tended to be granular (Plate 3.10). Nuclei of secondary spermatocytes undergo the second meiotic division to produce spermatids. The spermatids had small, elliptical nuclei and

developing tails (Plate 3.11). Mature spermatozoa were easily distinguishable. The helical heads were arrayed along the basement membrane with the tails extending towards the central lumen (Plate 3.12). After spermiation evacuated spermatocysts were visible in the region of the testis near the mesorchium (Plate 3.12). *Deania calceus* mature specimens had somewhat smaller spermatocysts at each stage of development, relative to the other species. Those containing spermatogonia ranged from 50 µm to 200 µm, while those with primary spermatocytes ranged from 160 µm to 250 µm. Spermatocysts containing secondary spermatocytes were in the size range 200 um to 300 µm, and those with spermatids 300 µm to 350 µm. Spermatocysts containing ripe spermatozoa were smaller than the spermatids, from 200 to 300 µm and evacuated spermatocysts ranged from 100 µm to 200 µm.

In mature specimens of *Centroscymnus coelolepis* the spermatocysts containing spermatogonia (Plate 3.13) ranged in diameter from 30 µmto 100 µm. The spermatocysts containing primary, secondary spermatocytes and spermatids ranged from 320 µm to 380 µm (Plates 3.14 – 3.16) and those containing ripe spermatozoa (Plate 3.17) from 260 µm to 320 µm, while evacuated spermatocysts were between 100 µm and 200 µm in diameter (Plate 3.18). Cross section of the testes of stage 1 *Deania calceus* and *Centrophorus squamosus* ripe spermatozoa were already evident, though in smaller numbers than in more mature fish (Table 3.30 and 3.31). In contrast ripe spermatozoa were not present in sections of stage 1 immature *Centroscymnus coelolepis* testes. Thus testes of the earliest stages of maturity in *Deania calceus* and *Centrophorus squamosus* contained ripe spermatozoa.

Mature specimens of *Centrophorus squamosus* had spermatocysts with spermatogonia (Plate 3.19) reached maximum size at 200 µm. The spermatocysts containing primary and secondary spermatocytes and spermatids (Plates 33.20 – 3.21) ranged in diameter from 200 µm to 300 µm. Spermatocysts containing ripe spermatozoa (Plate 3.22) were of similar size to the preceding sizes, but evacuated spermatocysts (Plate 3.23) ranged between 100 µm and 200 µm.

3.3 Age Estimation

3.3.1 External structure of the spines

Both *Centrophorus squamosus* and *Deania calceus* possess two dorsal fin spines, one on each dorsal fin. The spines are deeply inserted in the body of the shark, having their bases immediately above the vertebral column. The exterior portion of the spines of both species is shorter than the portion embedded in the musculature. The anterior (first) dorsal finspine in *Centrophorus squamosus* is shorter and wider, in the anterior-posterior axis. The second spine of *Centrophorus squamosus* is tall and narrow. The first spine of *Deania calceus* is narrow and short, while the second is tall and curved.

The external structure of the spine of *Centrophorus squamosus* is illustrated in Plate 3.24. The trunk, the main body of the spine, is deeply inserted in the body. The spine tapers to a fine tip. The cap is a thickened structure, entire only in the apical portion for either species. Proximally, it is reduced to 3 ribs, occupying the corners of the spine. The anterior rib of the cap is overlain with enamel in *Centrophorus squamosus*. In *Deania calceus* all 3 ribs of the cap have enamel overlay (Plate 3.25). The enamelloid is characterised by a series of bands, associated with indentation and pigmentation of the cap.

3.3.2 Internal structure of the spines

The internal structure of the 1st spine of *Centrophorus squamosus* is shown in Plate 3.26, and that of the 2nd spine in Plate 3.27. The trunk encloses the central lumen. In proximal sections the lumen is occupied by a cartilaginous rod, while in distal sections it is occupied by pulp. In cross-section the trunk can be seen to consist of two components, the inner and outer trunk layers. The thickness of the inner layer increased distally, while the outer remained of similar thickness along the length of the spine. The lumen of the spine was occupied by cartilage proximally, but in distal sections by pulp. In distal sections the lumen became constricted by the inner trunk layer. Separating the two trunk layers was the trunk primordium. Canaliculi traverse both trunk layers. Those in the inner layer lead from the lumen, while those in the

outer layer lead from the outer surface of the trunk. These canaliculi terminate either side of the trunk primordium. The inner trunk layer was characterised by a number of distinctive check marks. One such check was pronounced in *Centrophorus squamosus*. This check is similar to that defined as the discontinuity by Guallart Furio (1998). It was located near to the trunk primordium and led to the initial observation that the trunk was composed of 3 dentine layers, with the intermediate layer bounded by the trunk primordium and the discontinuity (Clarke *et al.*, 1998). These initial observations showed that the portion of the inner trunk layer bounded by the discontinuity and the lumen disappeared at the base of the external spine. This is because the discontinuity converged with the interior surface of the inner dentine at the external spine base. Guallart Furio (1998) also noted the disappearance of the discontinuity at the spine base. That the area of the trunk bounded by the discontinuity and the trunk primordium is not a separate dentine layer is evidenced by the canaliculi of the inner trunk layer, which traverse this mark. The presence of a check in the inner dentine led several authors to consider a third, intermediate, dentine layer (Holden and Meadows, 1962; Tanaka, 1990b). As noted by Guallart Furio (1998) none of these authors demonstrated how such an intermediate layer could form. The discontinuity appears to form as a result of the transition of the cellular bodies of the odontoblasts from a restricted position in the lumen, between the cartilage and the dentine to the relatively less restricted environment of the pulp filled lumen. This transition, which takes place as a result of growth of the spine upwards, is reflected by the change in direction of the canaliculi as they traverse the discontinuity (Guallart Furio, 1998).

The thickened portion of cap is composed of dentine and is termed the mantle. Within the mantle are vessels which are obvious in cross-section (Plate 3.26). The posterior face of the spines was concave, but there was no evidence of the glandular tissue located in this area of spines of young *Squalus acanthias* (Maisey, 1979). This gland secretes venom (Evans, 1943) and is thought to afford protection to young squaliform sharks (Maisey, 1979).

3.3.3 Spine Growth

The spine grows in thickness as a result of the action of odontoblasts in the inner and outer trunk layers, in the portion of the spine embedded in the fish. In the external portion of the spine odontoblasts are involved in the development of the inner trunk layer only. Growth of the inner trunk layer takes place all along the length of the spine, as evidenced by its narrowing of the lumen in distal sections. Growth in length of the spine takes place by dentinogenesis of both trunk layers at the base and also growth of the cartilage. Development of the enamelloid on the cap is the result of deposition of enamel and melanin at the base of the exterior spine. Some specimens exhibited white enamelloid bases and some dark. The banding pattern on the cap was described by Beamish and McFarlane (1985). These authors demonstrated that this pattern of pigmented ridges was a result of asynchrony between the deposition of pigment and enamelloid, and the growth of the trunk.

Regression coefficients were significantly different (ANOVA, $p < 0.05$) from zero in all cases, indicating that spine diameter increases with length. It seems reasonable, therefore, to conclude that the spines grow throughout the life of the fish. Allometric regression of spine base diameter on total length for both species using natural logarithm-transformed variables are presented in Table 3.32. In all cases the regression coefficients were < 1 but positive in sign. This indicates that spine growth is negatively allometric, the spines growing relatively smaller with increased TL. Results of ANCOVA indicated that in *Deania calceus*, regression coefficients for first and second spines were not significantly different for males ($p > 0.5$) or for females ($p > 0.3$). First and second dorsal spines of male *Centrophorus squamosus* also had homogeneous regression coefficients (ANCOVA, $p > 0.8$). Thus the mean rate of increase in base diameter of first and second dorsal spines were not significantly different, indicating that both spines grow at a similar rate with increasing TL.

3.3.4 Obtaining age estimates

Based on the conclusion that the spines increase in diameter throughout life and because they possess several banding patterns, they were considered as potentially useful for age estimation. Several patterns of bands are present on the spines of these species, which may be useful for estimating age. These are described below.

The enamelloid tissue of the cap in both species displayed a banding pattern, however the pattern was clearer in the case of *Centrophorus squamosus*. For comparative purposes the banding pattern on the cap of the spine of *Squalus acanthias* is shown in Plate 3.28 and for *Centrophorus squamosus* in Plate 3.29. Counts of banding on the cap of *Centrophorus squamosus* ranged from 10 to 42 and the pattern was clearest in the proximal portion of the spine, and less clear distally. However, in many cases a distinct check was obvious towards the tip. Plate 3.30 shows the indentation of the cap, possibly due to parturition. Its distal position suggests that it was formed early in the life history of the fish, probably as a result of parturition.

Age estimates obtained from annuli on the cap of *Squalus acanthias* spines were validated (McFarlane and Beamish 1987b). Based on the results of this study, and the structural similarities between the cap tissues of all squalid sharks the cap was considered as suitable for age estimation of *Deania calceus* and *Centrophorus squamosus* in this study. However, the annuli on the cap of *Centrophorus squamosus* (Plate 3.28) were not as clear as those of *Squalus acanthias*, the pigmentation was often faint, the ridges often worn and the base was in many cases damaged or gnarled, a gerontic condition according to Maisey (1979).

Age estimation was attempted, but it was not always possible to obtain complete counts, or to ascertain when a complete count had been obtained. There was a further problem due to loss of annuli due to wear at the tip. Had this been the only reason for loss of annuli it could have been corrected by using the method of Ketchen (1975) for worn *Squalus acanthias* spines. But because there were several causes of annuli-loss it was not possible to obtain age estimates. The annuli on the enamelloid of *Deania calceus* were less distinct than those of *Centrophorus squamosus* and the spines were subject to greater wear, being less robust. For these reasons and those cited for

Centrophorus squamosus it was decided not to proceed with counting the annuli on the cap of spines of *Deania calceus*. Bands on the cap of the spine of *Centrophorus granulosus* were described by Guallart Furio (1998) but were also found to be too obscure to count.

A series of ridges were present on the lateral faces of the mantle of *Centrophorus squamosus* spines and converged distally, suggesting that they were associated with the thickening of that component of the spine. There was no evidence of any banding in the anterior mantle in cross-section of *Centrophorus squamosus* spines. There was evidence of banding in the anterior mantle of *Deania calceus* spines. However in neither species were these structures used for age estimation.

The structure and banding patterns of the 2nd and 1st spines of *Centrophorus squamosus* are shown in Plates 3.26 and 3.27 respectively. Plate 3.32 shows the internal structure and banding pattern of 1st spine of *Deania calceus*, while that of the 2nd spine is shown in Plate 3.33. Bands in the outer and inner trunk layer were clearly visible in cross-sections as concentric translucent and opaque marks. The outer trunk layer only increases in thickness in the part of the spine embedded in the shark. Therefore only the inner dentine layer is likely to represent growth throughout the life of the shark. Counts of bands in the outer layer ranged from 2 to 18 in *Centrophorus squamosus* (Clarke, *et al.*, 1998). Counts in the outer layer increased in successively proximal sections to about one half the length of the external spine but decreased proximally. This demonstrates that banding in the outer trunk layer only represented a part of the life history of the shark.

Counts in the inner trunk layer were distinguishable in both species. Successively proximal sections taken at 2mm intervals produced increasing counts until a maximum was obtained at the point where the lumen became constricted. Maximum band count for both species was recorded in sections taken from the site where the lumen became constricted. Clearly, it is necessary to obtain sections from as near the tip as possible because sections from near the base would not represent growth during the early period of life (when the spine was shorter).

The inner trunk layer was chosen for age estimation in both species because it is the only component of the trunk which provides counts which were formed throughout the life of the fish. For the purposes of counts, one translucent and one opaque mark were considered as a band. While the band on the cap of *Centrophorus squamosus* spines (Plate 3.29) is probably annual, there was not sufficient clarity for clear differentiation between bands. McFarlane and Beamish (1987b) noted that the mark visible in cross section was also annual. However, they did not use these annuli for ageing, citing the difficulty in processing, the cap providing a much easier method, and because of the loss of bands due to wear at the tip. Holden and Meadows (1962) and Soldat (1982) noted that there was a danger that counts of annuli near the tip may miss some of the growth due to wear. The possibility of missing annuli in cross-sections too near the tip is illustrated in Plate 3.31 where inner dentine bands converge distally. The annuli appear to converge along the constricted lumen. The annuli are indistinguishable in this area and a section taken near the tip will produce a lower count than a more proximal section. In this study spines that were worn below the region of maximum band count in unworn spines, immediately proximal to the constriction of the lumen, were eliminated to avoid underestimation of age.

The age estimates for the species under study are based on the assumption that each band was formed annually and after birth. In the absence of gravid female *Centrophorus squamosus* it was not possible to study embryonic spines and there is no way of determining whether banding takes place in the embryonic phase. Only 2 female *Deania calceus* of maturity stage 6 were recorded however the embryos in both cases still had large external yolk sacs and unerupted dorsal spines, sections of which did not display any banding pattern. Guallart Furio (1998) used width measurements of the inner trunk layer of full-term embryos to estimate the extent of embryonic growth in the spines he used for age estimation of *Centrophorus granulosus*. This appears to be the only means by which to adjust age estimates for embryonic growth. However in the present study this is not possible due to the lack of full term embryos.

3.3.5 Readability and Precision

The number of spines for which age estimation was attempted is presented in Table 3.33 and the readability scores for *Centrophorus squamosus* in Table 3.34. In *Centrophorus squamosus* both spines produced readable cross-sections. However, in many cases the 1st spine was easier to read than the second. The annuli were more widely spaced and allowed for easier interpretation. Readability scores (Table 3.34) show that the first spine produced a greater percentage of readable cross-sections. However almost one fifth of first spines and one quarter of second spines were unreadable. In many cases check marks prevented counting of bands.

Cross-sections interpreted for age estimation of *Centrophorus squamosus* are shown in Plates 3.26 and 3.27. Cross-sections of 1st and 2nd spines of *Deania calceus* as used for age estimation are shown in Plates 3.32 and 3.33. Fig. 3.63 shows the differences in estimated age between 1st and 2nd spines for both species. The tendency for 2nd spines to produce greater counts in a proportion of cases could be construed as an indication that the 1st spine underestimates age. Holden and Meadows (1962) suggested that this was the case for *Squalus acanthias*. However, differences of more than one year only occurred in a small proportion of spine pairs. It seems reasonable to conclude that the differences are the result of a bias in the interpretation of the band patterns. The closer spacing of the annuli of the 2nd spine of *Centrophorus squamosus*, and the poorer definition in the pattern of banding of the 2nd spines of *Deania calceus* (Plate 3.33) resulted in difficulties in differentiating between annuli and checks or splits. All complete concentric bands were included in counts and no complete bands were rejected. First spines of *Deania calceus* produced cross-sections of better clarity (Plate 3.32).

Where both spines provided readable cross-sections for a fish, comparisons were made between the spine pairs in order to determine the level of precision of age estimation, and whether each spine produced the same counts. Of 28 spine pairs available for male *Centrophorus squamosus* 5 disagreed by 1 year and 2 by 2 years. Of 45 pairs of female spines 7 disagreed by 1 year, 3 by 2 years and 1 by 3 years (Fig. 3.63). Thus, for females there was 88 % agreement within ± 1 year and for males 93

% agreement within ± 1 year. In the case of *Deania calceus* females where 25 spines were available for comparison there were 3 which disagreed, all by one year. Of 32 male *Deania calceus* pairs 4 disagreed by 1 year and 2 by 2 years (Fig 3.65). Thus, for females 100 % agreement was obtained within ± 1 year, while the corresponding percentage for males was 93 %.

Examining a set of age estimates (in this case a pair) for a sample of fish does not evaluate the degree of precision equally for all species. This was demonstrated by comparing Pacific cod with spurdog *Squalus acanthias* (Beamish and Fournier, 1981). These authors noted that agreement of 95 % within ± 1 year for cod was in fact poor precision because of the small number of age groups in that species, whereas the same percentage of agreement within ± 5 years for *Squalus acanthias* was indeed good precision, because of the latter species' great longevity.

In order to compare spine pair band counts the average coefficient of variation, CV (Campana *et al.,* 1995) was employed, which expresses the standard deviation as a percentage of the mean age estimated from a spine pair. CV was 0 in the majority of cases, where the spine pairs had the same count. It varied from 0 to 5.65 for female *Centrophorus squamosus* and the average CV across the entire sample of paired age estimates was 0.67. In the case of male *Centrophorus squamosus* the range was from 0 to 5.43 (mean = 0.59). In *Deania calceus* females the range was between 0 ad 4.56 (mean = 0.51) and for males the mean CV was 2.25 with a range of values from 0 to 23.32. While the CV for some spine pairs were high (up to one quarter of the mean in one case) the majority were quite low or 0 and the average values were small. Therefore it the age estimation procedures employed gave a reasonable degree of precision.

A review of other verification studies in elasmobranchs was completed by Cailliet (1990). Among the verification techniques considered by these authors were length-frequency analysis, edge analysis, laboratory growth studies, field growth studies, radiometric ageing, microanalysis and back calculation. Studies of growth, whether in the field or in the laboratory, radiometric and micro-analytical techniques were all beyond the scope of this study. Edge analysis was not considered possible because of

the incomplete dentinogenesis along the interior of the inner trunk layer. Radiometric and micro analytical techniques were also beyond the scope of this study. Of the remaining techniques length-frequency analysis could be considered as a possible option. But mean length showed no significant increase with increasing estimated age in *Centrophorus squamosus*. In *Deania calceus* there was some evidence of an increase in mean length between estimated ages 15 to 18 but no increase for subsequent estimated age groups. It seems unlikely, therefore, that length frequency analysis, such as ELEFAN (Pauly, 1987) could segregate length modes in the distributions of these species. Length frequency analysis has been more successful for smaller and younger elasmobranchs (Cailliet, 1990) but no smaller (or younger) specimens of any of the species were present in the study area. Back calculation is a technique that uses a set of measurements from a fish to infer its length at earlier times (Francis, 1990). This technique has been used in the past for comparison with other age estimation data, but it can not be used to determine if a band is an annual mark or not (Cailliet *et al.*, 1986). Back calculation of length at previous age has been used where there is an absence of smaller specimens in a growth study (Yudin and Cailliet, 1990; Simpfendorfer, 1993) and it has been used widely in otolith studies (Francis, 1990). However Williams and Bedford (1974) cautioned that back calculation couldn't be conducted accurately if applied to otolith sections. A series of sections of an otolith show considerable differences in both shape of the otolith and the size of the bands (Williams and Bedford, 1974). However back calculation has been applied to sectioned centra to estimate size at previous ages (Branstetter, 1987; Branstetter *et al.*, 1987; Casey *et al.*, 1985; Martin and Cailliet, 1988; Yudin and Cailliet, 1990 and would not lead to inaccuracies because the centrum is subject to appositional growth (Walker *et al.*, 1995). However in the case of dorsal spines back calculation is not applicable for the same reasons as described for sectioned otoliths by Williams and Bedford (1974).

No validation of age was carried out in this study. The precision of the age estimation method was analysed, and results indicate a reasonable degree of reproducibility. Cailliet and Tanaka (1990) recommend that age estimation of squalid sharks be verified by cross-comparisons between structures. In the present study this requirement was fulfilled by comparisons between the 2 dorsal spines. Vertebrae have proven unsuitable for age estimation in the present study. Previous studies of

squalid sharks also found vertebrae to be unsuitable for age estimation (Soldat, 1983; Cailliet *et al.*, 1983 and Polat and Gumus, 1995), or the results obtained were inconclusive (Jones and Geen, 1977a).

Table 3.32. Results of allometric regression analysis of spine base diameter on TL using natural logarithmically transformed variables. Standard error (S.E.) of regression coefficient (b) given in each case, along with regression intercept.

Species	Sex	Spine	n	a	b	S.E.
Centrophorus squamosus	male	1st	66	-0.34	.58	.185
		2nd	33	-0.52		
	female	1st				
		2nd				
Deania calceus	male	1st	54	-1.11	.67	.338
		2nd	38	-1.1433		
	female	1st	45	0.757	0.25	.12
		2nd	45	0.502		

Table 3.33. Numbers of fin-spines of squalid sharks for which age estimation was attempted.

Species	**Method**	**First Spine**	**Second Spine**
Centrophorus squamosus	Whole	154	65
Centrophorus squamosus	Sectioned	157	99
Deania calceus	Sectioned	160	147

Table 3.34. Readability of sectioned fin-spines of *Centrophorus squamosus*.

Score	**First spine**	**Second spine**
Easy	7 %	5 %
Readable	64 %	61 %
Readable with difficulty	10 %	12 %
Unreadable	19 %	22 %
	n = 157	**n = 99**

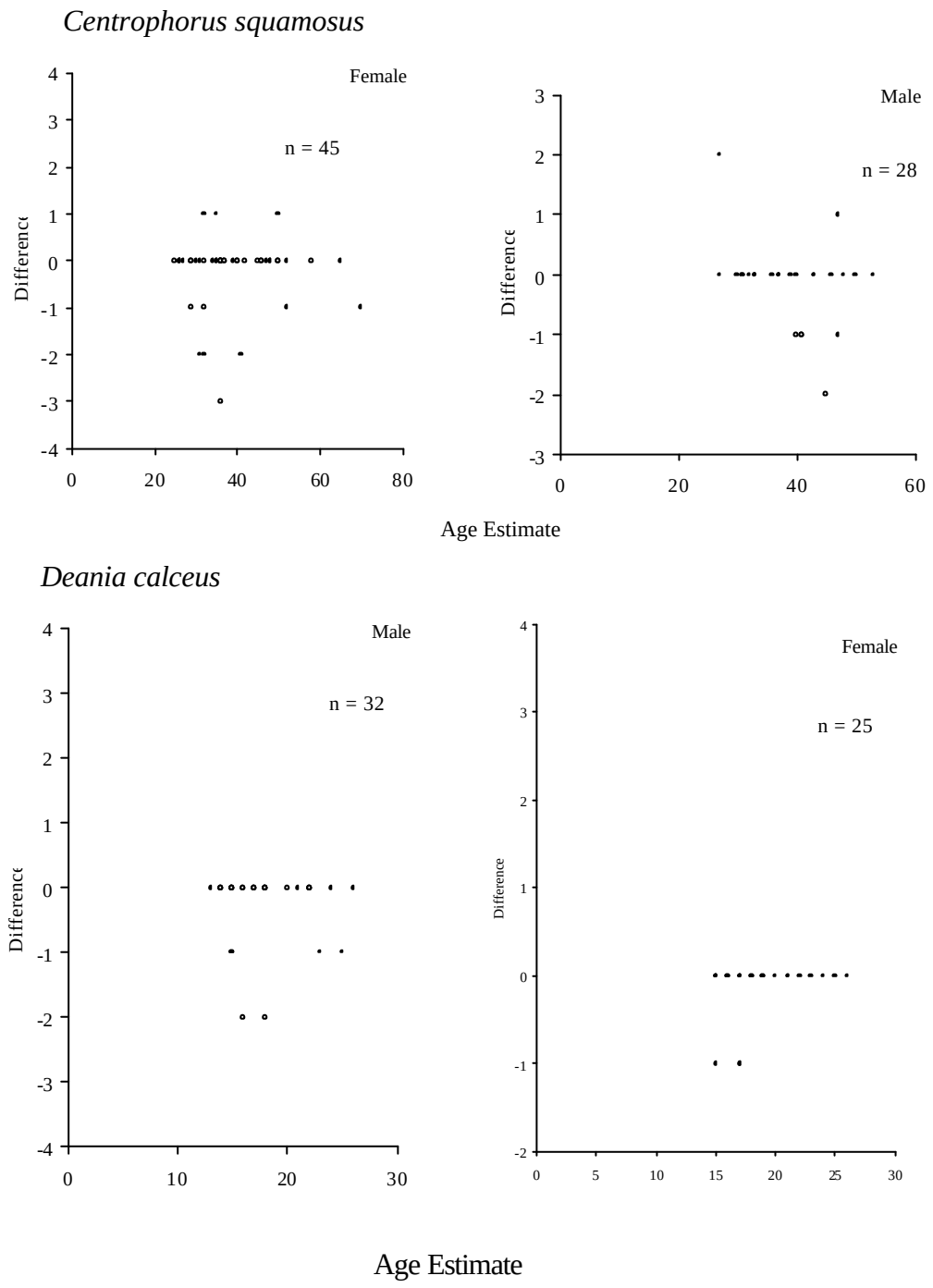

Fig. 3.63. Differences (years) in estimated ages between spine pairs of *Centrophorus squamosus* and *Deania calceus*. Each point represents one fish for which both spines were read.

3.3.6 Empirical growth

Age estimates for 1st and 2nd dorsal spines of female *Centrophorus squamosus* are presented in Table 3.35 and Table 3.36 respectively and the corresponding data for males are presented in Tables 3.37 and Table 3.38 for males and females respectively. The estimates of age for female and male *Deania calceus* from 1st dorsal spines are given in Table 3.39 and Table 3.40 respectively. Age estimates of female and male *Deania calceus* from 2nd dorsal spines are given in Table 3.41 and Table 3.42 respectively.

Since a reasonable degree of precision was found between spines it was decided to use 1st dorsal spines of both species for age estimation and those from the second spines for comparative purposes. Empirical growth curves for female and male *Centrophorus squamosus* are shown in Fig. 3.64 and Fig. 3.65 respectively. Empirical growth data for *Deania calceus* from first dorsal spines are shown in Fig. 3.66 and Fig. 3.67 for females and males respectively. Estimated ages for female *Centrophorus squamosus* ranged from 21 to 70 years for 1st spines and 25 to 71 years for 2nd spines. There was a noticeable trend for increased size with increased age (Fig. 3.66). However ANOVA did not detect any significant difference ($P > 0.3$) in mean length at age for any estimated age group where $n > 4$ indicating that growth in female *Centrophorus squamosus* had slowed down or ceased. The lack of evident growth in length or weight of female *Centrophorus squamosus* seems surprising in view of the small numbers of mature specimens in the study area. However there was evidence to show that some females not exhibiting signs of maturity had already carried pups (Section 3.2.4), and it appears that somatic growth had ceased before the onset of sexual maturity in this species.

Age estimates from 1st spines for male *Centrophorus squamosus* ranged from 21 to 53 years. From 2nd spines the estimates were in the range 15 – 53 years. There was little evidence of an increase in length or weight with increasing estimated age for either spine. Results of ANOVA showed no significant difference ($p > 0.3$) in mean length at age for any estimated age group where $n > 4$. This indicates that the male population of *Centrophorus squamosus* was no longer undergoing any appreciable growth. This is in agreement with the frequency of occurrence of maturity that showed

that most males at all depths were mature. With regard to females it is likely that many of the specimens which appeared to be "virgin ripening" were in fact post-natal in a resting period. This agrees with the lack of growth in the population. Mature females either about to ovulate or resting after parturition are unlikely to grow.

No *Centrophorus squamosus* less than 80 cm were ever recorded during this study. Furthermore, no specimens were estimated to be less than 21 years of age. Recently a near-term embryo of *Centrophorus squamosus* was secured from Madeira (Hareide and Stehmann *pers. comm*.), which was 33 cm TL and still had an external yolk sac. It may be assumed that *Centrophorus squamosus* are born at greater TL. Thus specimens of both sexes of between at least 33 cm and 80 cm are absent from the study area. It is possible that *Centrophorus squamosus* may grow about 2 cm every year prior to their arrival in this area.

Age estimates for female *Deania calceus* ranged from 11 to 35 years for 1st spines and 13 to 31 years from second spines. For males 1st spine yielded estimates in the range 13 to 29 years and 2nd spine estimates of 13 to 32 years. In *Deania calceus* there was a trend for females of greater estimated age to be of larger size based on readings of both spines. Results of ANOVA showed some evidence of increased mean length at age ($p = 0.06$) for estimated age groups 15 to 18, indicating a small degree of growth between ages 15 and 18, with growth ceasing thereafter. While it was not possible to estimate age at 50 % maturity, owing to poor representation of certain age groups, the TL_{50} of 105 cm for female *Deania calceus* corresponds to estimated age of 25 years. This suggests that growth had slowed down or ceased with onset of maturity in the population. In the case of males there was no evidence of increased size at age. Results of ANOVA indicated no significant difference ($p > 0.3$) in mean length at any estimated age where $n > 4$, suggesting that growth in the male population had ceased.

Age estimation data from the current study, from 1st dorsal spines, was combined with the data published in graphical form by Machado and Figueiredo (2000) derived from 2nd dorsal spines in order to obtain estimates of the von Bertalanffy Growth Function (VGBF). Inspection of the cross-sections in Machado and Figueiredo's study showed that their interpretation of the inner and outer dentine layers was not the same as that

adhered to in the present work. These authors appeared to count the outer trunk layer as an annulus (Machado and Figueiredo, 2000, Fig. 2 d). For comparative purposes an adjustment was made by subtracting one year from each of their age estimates before combining the data.

Estimates of the parameters of the von Bertalanffy Growth Function are presented in Table 3.43. and Fig. 3.68. show the fitted VBGF for males and females respectively. The VBGF model appeared to fit the combined data sets well for both sexes. The value of asymptotic length, L_∞, was much higher for females, which is in agreement with their larger size. The asymptotic length for females agreed well with the largest females measured. While the asymptotic length of males was lower than the greatest maximum length observed, it did fit the data range for large males well. Females had substantially lower value of K than males, indicating that they are slower growing and take a longer period of time to reach asymptotic length. Estimates of K and L_∞ based on both published and the adjusted Portuguese data are broadly similar. However the adjusted data produced a more meaningful estimate of t_0 since Squalidae are known to have long gestation periods (Clark, 1922; Templeman, 1944). However the two data sets appear to fit better when the Portuguese data is adjusted. Furthermore, collaborative age estimation work should be carried out in order that a single protocol be formulated. However the combination of the two data sets allowed for first estimates of the VGBF in this species.

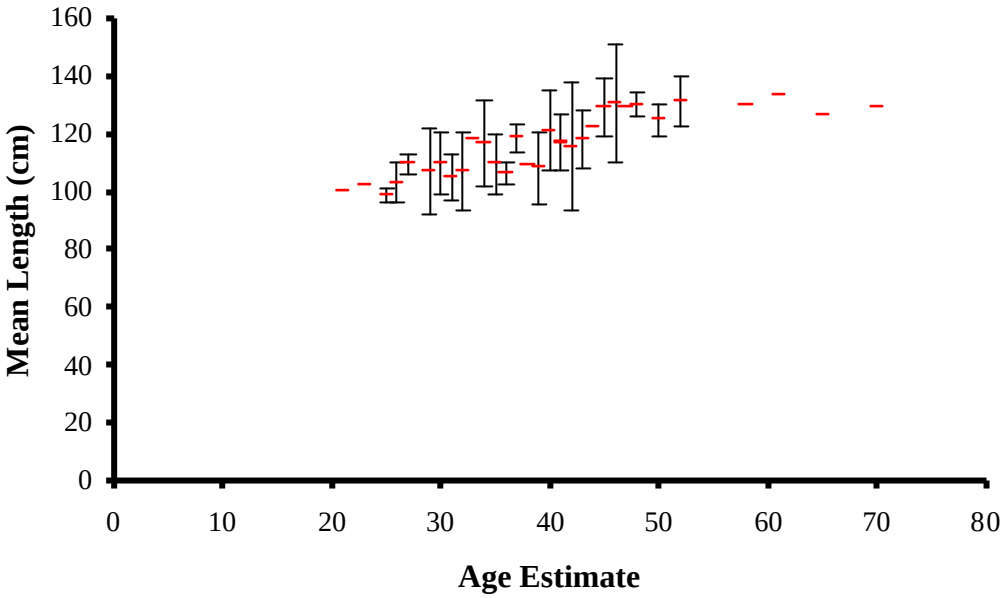

Fig. 3.64. Empirical growth of female *Centrophorus squamosus* based on mean length ± 1 SD, at estimated age from 1st dorsal spines, n = 66.

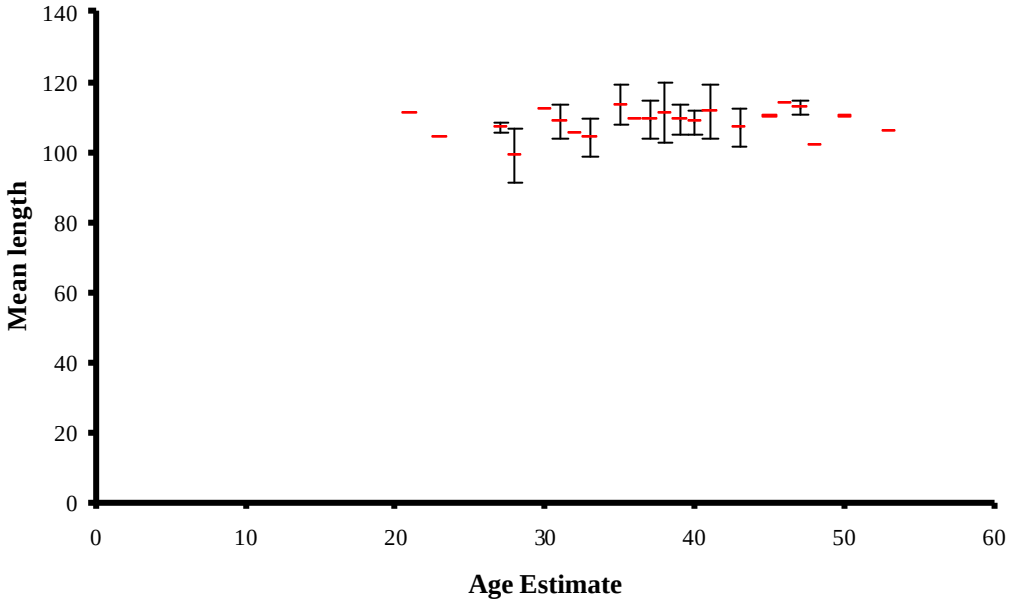

Fig. 3.65. Empirical growth of male *Centrophorus squamosus* based on mean length ± 1 SD, at estimated age from 1st dorsal spines, n = 61.

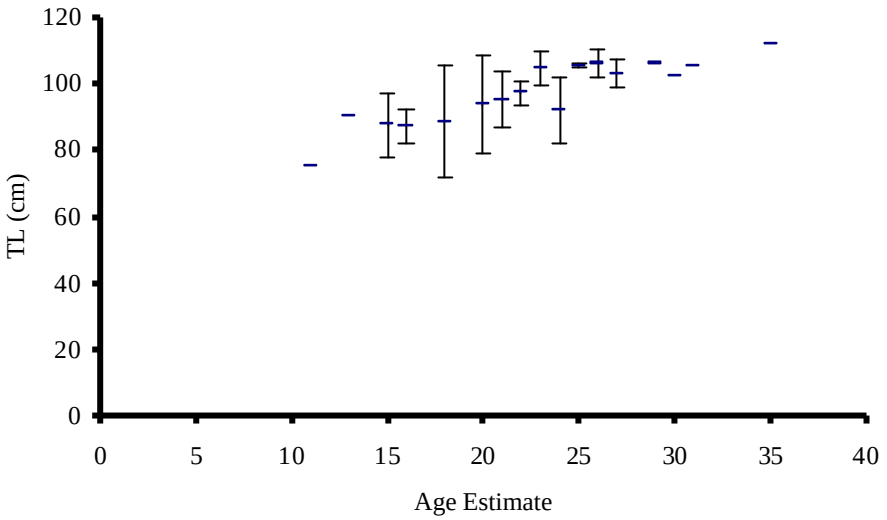

Fig. 3.66. Empirical growth of female *Deania calceus* based on mean length ± 1 SD at estimated age of 1st dorsal fin spines, n = 49.

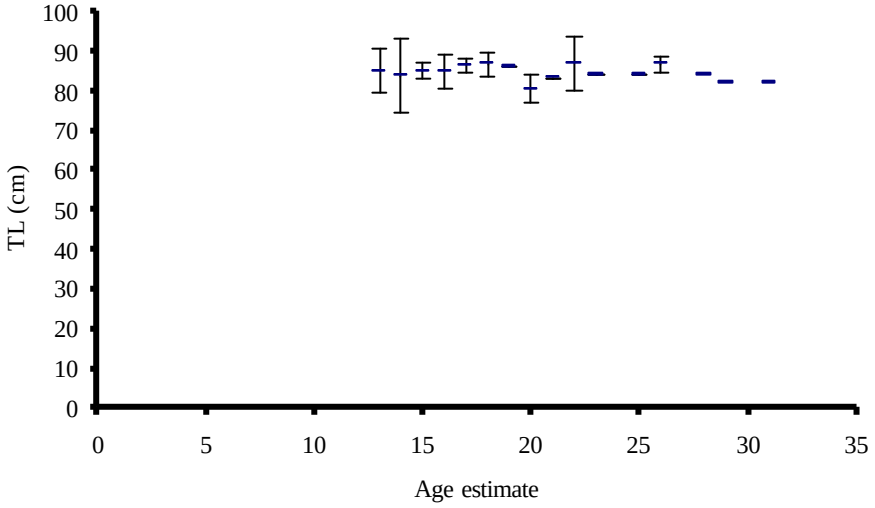

Fig. 3.67. Empirical growth of male *Deania calceus* based on mean length ± 1 SD at estimated age from 1st dorsal fin spines, n = 64.

Table 3.35. Mean observed length (cm) and weight (g) at each age group estimated from 1st dorsal fin-spines of female *Centrophorus squamosus*, S.D. sample standard deviation.

	Total length (cm)			Round Weight (g)			Gutted Weight (g)		
Age Group	**n**	**Mean**	**S.D.**	**n**	**Mean**	**S.D.**	**n**	**Mean**	**S.D.**
21	1	100.0		1	5360				
23	1	102.0		1	5340				
25	2	98.5	2.12	2	7800	2998.13	1	4200	
26	4	103.0	7.12	4	5955	1170.00	2	4600	
27	2	109.5	3.54	2	7320	311.13	1	5380	
29	3	107.0	15.10	3	6487	2283.11	2	3900	1979.90
30	2	109.5	10.61	2	6970	2588.01	1	4240	
31	3	104.7	8.02	3	6500	1950.08	2	4110	1032.38
32	4	106.8	13.60	4	6640	1893.09	2	4875	2722.36
33	1	118.0		1	9200		1	6200	
34	2	116.5	14.85	2	10050	5529.58			
35	5	109.4	10.26	5	7552	1999.03	4	5154	872.38
36	5	106.2	4.09	5	6524	815.16	5	4624	636.14
37	2	118.5	4.95	2	6905	1562.71	1	5000	
38	1	109.0		1	7100				
39	2	108.0	12.73	2	6540	2206.17	1	6100	
40	3	121.0	13.89	3	10195	3450.01	2	6950	2474.87
41	2	117.0	9.90	2	10400	3959.80	2	7380	2573.87
42	2	115.5	21.92	2	10010	6943.79	1	3800	
43	2	118.0	9.90	2	9155	4320.42			
44	1	122.0		1	12820				
45	2	129.0	9.90	2	10950	1484.92	1	7700	
46	2	130.5	20.51	2	15993	10164.66	1	14620	
47	1	129.0		1	11300		1	8140	
48	2	130.0	4.24	2	16530	3662.81	2	10910	947.52
50	3	124.7	5.51	3	11297	2513.65	1	7220	
52	2	131.0	8.49	2	16600	2121.32	2	11025	1661.70
58	1	130.0		1	15800		1	10200	
61	1	133.0		1	15970				
65	1	126.0		1	15200		1	10550	
70	1	129.0		1	13940		1	9460	

Table 3.36. Mean observed length (cm) and weight (g) at each age group estimated from 2nd dorsal fin-spines of female *Centrophorus squamosus*, S.D. sample standard deviation.

	Total length			Round weight			Gutted Weight		
Age group	**n**	**Mean**	**S.D.**	**n**	**Mean**	**S.D.**	**n**	**Mean**	**S.D.**
24	1	98		1	4550		1	3500	
25	1	100		1	5680		1	4200	
26	4	110.5	8.70	4	8265	3572.80	2	4600	
27	1	107		1	7100		1	5380	
29	3	118.7	12.10	3	9324	3575.03	1	5300	
30	2	97.5	6.36	2	4840	424.26	2	3370	1230.37
31	3	114.3	19.86	3	7180	2902.48	1	3380	
32	1	112		1	7930				
33	2	95.5	12.02	2	5215	1788.98	2	3895	1336.43
34	4	117.3	9.64	4	9255	3152.20	3	6454.7	1013.15
35	3	113.3	14.01	3	9306.7	5130.00	3	6266.7	2767.26
36	4	107	4.24	4	6470.0	930.88	4	4665	726.89
37	2	118.5	4.95	2	6905.0	1562.71	1	5000	
38	3	121.3	24.54	3	10090.0	4737.22	2	6110	3804.23
39	2	110.0	9.90	2	7420.0	961.67	2	5280	1159.66
40	3	118.7	9.87	3	12795.0	7914.64	2	9400	5939.70
42	3	116	13.08	3	10323.3	4022.14	2	5475	318.20
43	1	110		1	7600.0		1	5560	
45	1	122		1	12000.0		1	7700	
46	2	130.5	20.51	2	15992.5	10164.66	1	14620	
47	2	127	2.83	2	12170	1230.37	2	8840	989.95
48	2	130	4.24	2	16530	3662.81	2	10910	947.52
49	1	122		1	10380		1	7220	
50	2	126	7.07	2	11755	3372.90			
52	1	137		1	18100		1	12200	
53	1	125		1	15100		1	9850	
54	1	110		1	8315				
55	1	120		1	15000		1	9000	
58	1	130		1	15800		1	10200	
65	1	126		1	15200		1	10550	
68	1	130		1	12790				
71	1	129		1	13940		1	9460	

Table 3.37. Mean observed length (cm) and weight (g) at each age group estimated from 1st dorsal fin-spines of male *Centrophorus squamosus*, S.D. sample standard deviation.

	Total length			Round weight			Gutted Weight	
Age group	n	Mean	S.D.	n	Mean	S.D.	n	Mean	S.D.
21	1	111		1	7560				
23	1	104		1	5195				
27	2	107	1.41	2	6865	572.76	1	4860	
28	3	99	7.94	3	5453.3	884.61	1	3800	
30	1	112		1	7600.0		1	5550	
31	3	108.7	4.62	3	6606.7	1010.41	2	4580	141.42
32	1	105.0		1	5940.0		1	4480	
33	4	104.0	5.48	4	6338.8	1366.43	2	4310	1371.79
35	3	113.3	5.69	3	7960	1045.18	1	5700	
36	1	109.0		1	6580		1	4980	
37	5	109.2	5.63	5	6776	935.35	3	5263.3	886.25
38	2	111.0	8.49	2	7070	1456.64			
39	2	109.0	4.24	2	7110	636.40	2	5320.0	424.26
40	2	108.5	3.54	2	6585	459.62	1	4560.0	
41	2	111.5	7.78	2	7122.5	1071.27	1	5640.0	
43	4	106.8	5.50	4	6038.5	590.13	3	4486.7	560.12
45	1	110		1	6600		1	4920	
46	1	114		1	7540		1	5640	
47	2	112.5	2.12	2	7590	42.43	2	3860	1923.33
48	1	102		1	5620		1	4240	
50	1	110		1	6880		1	4840	
53	1	106		1	6220		1	4780	

Table 3.38. Mean observed length (cm) and weight (g) at each age group estimated from 2nd dorsal fin-spines of male *Centrophorus squamosus*, S.D. sample standard deviation.

	Total length			Round weight			Gutted Weight	
Age Group	n	Mean	S.D.	n	Mean	S.D.	n	Mean	S.D.
25	1	108		1	7270				
27	1	106		1	6460		1	4860	
30	1	112		1	7600		1	5550	
31	3	107.7	2.89	3	6353.3	593.41	2	4580	141.42
32	1	105.0		1	5940		1	4480	
33	5	103.8	4.76	5	6171	1241.39	3	4240	977.55
36	1	109.0		1	6580		1	4980	
37	3	111.7	3.21	3	7000	1126.94	3	5263.3	886.25
39	1	112.0		1	7560		1	5620	
40	1	106		1	6260		1	4560	
41	1	111		1	6910				
42	2	111.5	7.78	2	7122.5	1071.27	1	5640	
43	2	111.5	0.71	2	6367	555.79	1	5040	
46	2	112.5	2.12	2	7550	14.14	2	5430	296.98
47	1	110		1	6600		1	4920	
48	2	108	8.49	2	6620	1414.21	2	3370	1230.37
50	1	110		1	6880		1	4840	
53	1	106		1	6220		1	4780	

Table 3.39. Mean observed length (cm) and weight (g) at each age group estimated from 1st dorsal fin-spines of female *Deania calceus*, S.D. sample standard deviation.

	Length			Weight		
Age Group	**n**	**Mean**	**S.D.**	**n**	**Mean**	**S.D.**
11	1	75		1	1420	
13	1	90		1	3240	
15	6	87.33	9.42	6	2729.17	1111.21
16	4	87.00	4.97	4	2656.25	427.62
17	10	92.50	10.95	12	3552.92	1168.42
18	4	88.50	16.98	4	3637.50	512.14
19	2	104.00	1.41	2	5019.00	538.82
20	2	93.50	14.85	2	3170.00	806.10
21	2	95.00	8.49	2	3390.00	1852.62
22	3	97.00	3.61	3	3186.67	880.30
23	2	104.50	4.95	2	4832.50	116.67
24	2	92.00	9.90	2	3465.00	1605.13
25	3	105.33	0.58	3	5128.33	950.58
26	2	106	4.24	2	5375	49.50
27	2	103	4.24	2	5730	1428.36
29	2	106	0.00	2	6120	183.85
30	1	102		1	4960	
31	1	105		1	5970	
35	1	112		1	6820	

Table 3.40. Mean observed length (cm) and weight (g) at each age group estimated from 1st dorsal fin-spines of male *Deania calceus*, S.D. sample standard deviation.

	Length			Weight		
Age Group	**n**	**Mean**	**S.D.**	**n**	**Mean**	**S.D.**
13	4	84.75	5.50	4	2151	252.32
14	4	83.75	9.22	4	2146.25	713.67
15	10	84.90	2.08	11	2294.55	200.31
16	8	84.75	4.30	8	2286.88	239.15
17	9	86.22	1.72	9	2258.33	223.93
18	10	86.60	2.91	10	2327	342.71
19	1	86.00		1	2220	
20	3	80.33	3.51	3	1990	357.91
21	2	83.00	0.00	2	2325	106.07
22	4	86.75	6.85	4	2480	125.70
23	1	84.00		1	1980	
24	2	94.00	2.83	2	3004	76.37
25	1	84.00		1	2200	
26	2	86.50	2.12	2	2505	7.07
28	1	84.00		1	2220	
29	1	82		1	1880	
31	1	82		1	2190	

Table 3.41. Mean observed length (cm) and weight (g) at each age group estimated from 2nd[t] dorsal fin-spines of female *Deania calceus*, S.D. sample standard deviation.

	Length			Weight		
Age Group	**n**	**Mean**	**S.D.**	**n**	**Mean**	**S.D.**
13	1	86		1	2652	
15	4	82.75	14.62	4	2221.25	426.97
16	4	88.50	11.78	4	3012.50	1480.26
17	5	87.40	11.34	5	2926.00	1273.71
18	6	91.67	1.41	6	3228.33	897.63
19	2	104.00		2	5019.00	538.82
20	1	104.00	6.11	1	3740.00	
21	3	95.67	4.16	3	3560.00	1342.68
22	3	97.67	3.61	3	4303.33	992.99
23	3	104		2	5025.00	388.91
24	1	99		1	4600	
25	2	101		2	5725	601.04
26	1	109		1	5340	
29	1	81		1	2650	

Table 3.42. Mean observed length (cm) and weight (g) at each age group estimated from 2nd[t] dorsal fin-spines of male *Deania calceus*, S.D. sample standard deviation.

	Length			Weight		
Age Group	**n**	**Mean**	**S.D.**	**n**	**Mean**	**S.D.**
13	1	86		1	2434	
14	5	87.40	1.67	5	2430	174.36
15	6	84.67	1.97	6	2239.17	113.95
16	5	83.60	1.14	5	2308.00	164.53
17	4	84.75	1.26	4	2270.00	173.97
18	8	85.88	3.14	8	2386.25	251.79
19	2	87.00	7.07	2	2543.00	193.75
20	4	84.25	3.69	4	2526.50	491.74
21	6	84.83	3.25	7	2582.86	718.60
22	5	85.20	7.09	5	2318	243.35
24	2	88.00	5.66	2	2465	685.89
25	1	87.00		1	2600	
26	3	86.33	2.08	3	2400	173.21
32	1	83		1	1960	

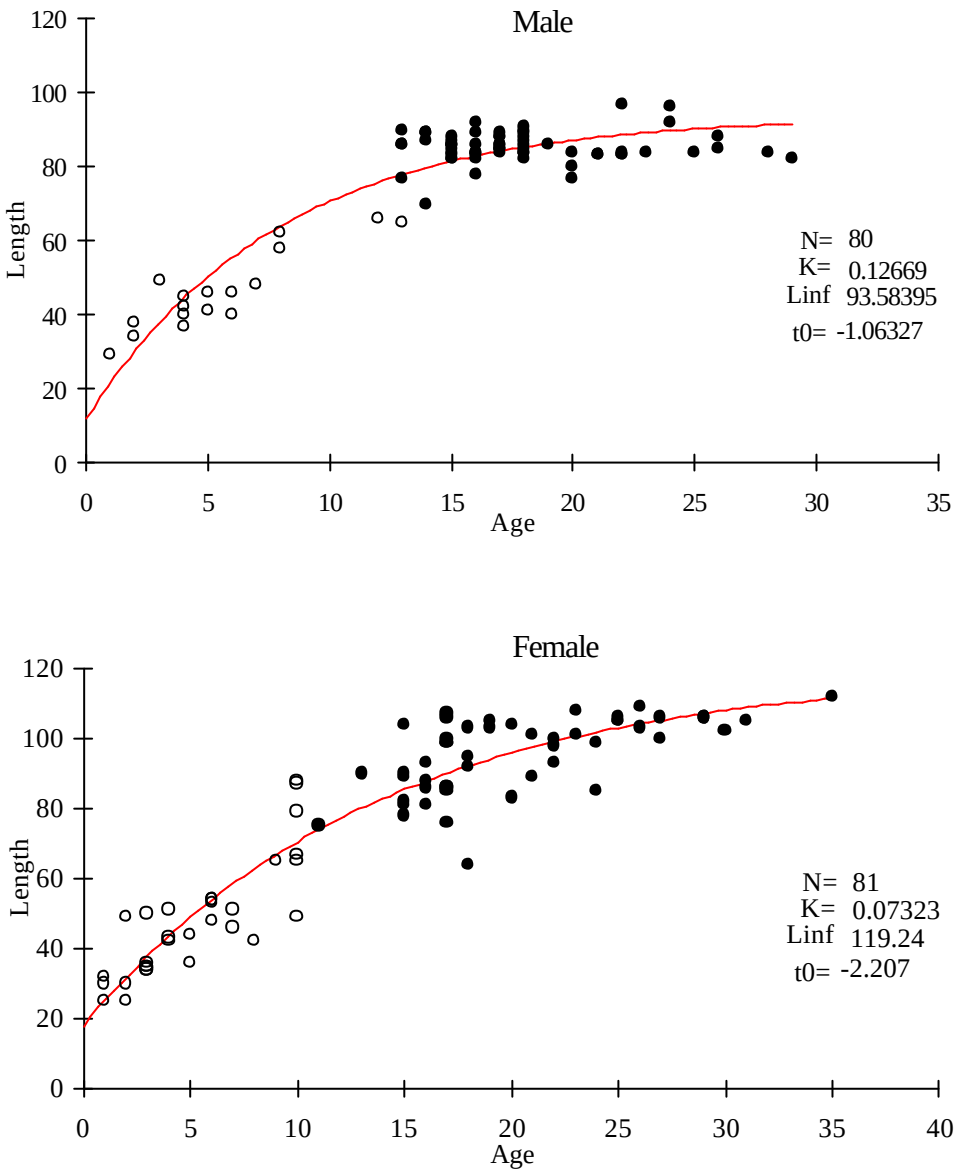

Fig. 3.68. Relationship between estimated age and length for *Deania calceus*. Open circles represent Portuguese data as presented in graphical form in Machado and Figueiredo (2000) and closed circles data from the present study. Von Bertalanffy growth curve fitted to the data using Marquardt's algorithm,

Table 3.43. Estimates of the parameters of the von Bertalanffy growth model for *Deania calceus* based on age estimation data from the first dorsal spine in the present study and from empirical growth data presented by Machado and Figueiredo (2000) and adjusted by subtraction f 1 year from age estimates. Growth parameters based on unadjusted age estimates from the latter study indicated by asterisk.

Females	**Estimate**	**S.E.**	**95 % confidence limits**	
K	0.073	0.1222	0.048	0.097
t_0	-2.207	0.7241	-3.649	-0.766
L_∞	119.24	6.7702	105.761	132.718
Males				
K	0.126	0.1751	0.9183	0.1615
t_0	-1.063	0.5627	-2.183	0.057
L_∞	93.583	2.7663	88.075	99.092
Females *				
K	0.077	0.0126	0.052	0.102
t_0	-0.933	0.6809	-2.289	0.422
L_∞	119.303	6.6700	106.024	132.582
Males *				
K	0.135	0.0190	0.098	0.173
t_0	0.165	0.5433	-0.917	1.247
L_∞	93.516	2.8231	87.895	99.138

3.4 Mortality

Catch curves for male and female *Deania calceus* are given in Fig. 3.69. The results of regression analysis of descending limb of the natural logarithm-transformed catch numbers at estimated age are contained in Table 3.44. Total instantaneous mortality rate (Z) was estimated for both sexes in *Deania calceus*. In both cases the descending limb of the curve was not smooth, with fluctuations in the logarithmically transformed catch numbers. The catch curves had so many estimated age groups present leading to these fluctuations. Archibald *et al*. (1981) working on deepwater redfish (*Sebastes*) species, also noted the fluctuations in numbers across the large number of age groups in these long-lived species. This may be attributable to variations in recruitment or variable fishing mortality over time (Archibald *et al.*, 1981). For both sexes the oldest estimated age groups displayed elevated catch numbers, indicating lower mortality. Archibald *et al*. have suggested that such data may indicate a decrease in the mortality rate for older fish prior to the onset of major senescent mortality. However in the present study it may reflect the relatively greater proportion of large specimens caught on long-lines. Comparison of the length-frequencies of female *Deania calceus* (Fig. 3.20) shows that large females not caught by trawls were present in long-line catches. The tendency for larger specimens of some fish to out–compete smaller specimens for baited hooks has been documented by (Bjordal and Lokkeborg, 1996).

Thus larger *Deania calceus* may out-compete smaller specimens for baited hooks. If larger fish are increasingly vulnerable to a given gear then older fish will tend to be over-represented in samples and estimates of survival too large (Ricker, 1975). Therefore the elimination of these oldest fish from estimates of total mortality seems justified. Rollefsen (1953) working on cod *Gadus morhua* in the Lofoten Islands found that of the fishing gears in use, purse seines, the most recent method, selected larger specimens than either trawls or long-lines. The increase in the overall rate of fishing, due to the purse seines, was cited by Ricker (1975) as a reason for the concave catch curves presented by Rollefsen. Ricker surmises that concave catch curves, with elevated catch numbers at advanced age, may be the result of a decrease in the rate of mortality, but are more likely the result of a recent increase in the rate of exploitation. The latter explanation may be more applicable to *Deania calceus* where fishing, by long-lines, only began in the 1990s (Iglesias and Paz, 1995; Pineiro *et al.*, 1998).

Estimates of mortality and survivorship (S) are presented in Table 3.45. Female numbers at estimated age are somewhat variable. Estimated age at first recruitment was taken to be 15 years for both sexes. This corresponded to the peak in the catch curve. Estimated age groups younger than 15 were considered to be only partially recruited. Thus total mortality was based only on fully recruited estimated age groups. The oldest groups were not included in calculations of Z either. This is because they tended to have lower mortalities than adjacent younger groups, and were eliminated in line with the procedure of Archibald, *et al*. (1981). These authors also eliminated the oldest age groups from their calculation of Z, citing that mortality in these fish was slightly lower, just prior to major senescence. Total mortality was estimated for 95.8 % of fully recruited males and 91.3 % of fully recruited females in the catch. Some of the age groups were poorly represented in the catches across the large number of ages. Total mortality of 0.239 for females is broadly comparable with 0.301 for males, the higher values of which indicate their shorter life span. These estimates of mortality only represent the range of estimated age indicated. No extrapolation for younger ages is permissible in regression analysis (Sokal and Rohlf, 1995). These estimates of mortality and survivorship represent only a portion of the total population. However they probably relate to the area of greatest fishing pressure on this species in the NE Atlantic.

Natural mortality (M) was estimated for *Deania calceus* by Pauly's (1980) equation, based on von Bertalanffy Growth Function parameters and ambient temperature. Estimates were also obtained by assuming that M was the level of mortality required to reduce the oldest age group in the population to 1 % of its initial size. This method was used for both *Deania calceus* and *Centrophorus squamosus*. Estimates from both methods (Table 3.45) were broadly similar, lower values for females reflecting their greater longevity. As Rago *et al.* (1998) pointed out M has not been estimated directly for many elasmobranchs. The availability of age estimate data allowed for first estimates of natural mortality in these species in the NE Atlantic. The estimates of M for *Deania calceus* are of similar value to those of cod (0.2) in the north Atlantic (Anon., 1998), suggesting that current estimates for may be too high. Estimates for *Centrophorus squamosus* were lower and in the expected range for a long-lived species. Fishing mortality (F) estimates for *Deania calceus* were slightly higher than

those of M for females, suggesting that fishing mortality has reached the levels of natural mortality. Estimates of F were somewhat lower than M for males. In the absence of the parameters of the von Bertalanffy Growth Function, it was not possible to estimate F for *Centrophorus squamosus* by the Pauly (1980) method.

In the case of *Centrophorus squamosus* natural mortality was only estimated by means of maximum age (King, 1995) since VBGF parameters were not estimable in the absence of information on smaller individuals. The estimates of M for males and females, 0.09 and 0.06 were based on the estimated oldest specimens in samples. This method implies that successive increases in maximum age produce successively smaller increments of M. This method was used by Rago *et al*. (1998) to estimate natural mortality of *Squalus acanthias*. The advanced ages attained by this species lead to the low values of M obtained. Thus for species that are estimated to be long-lived such as *Centrophorus squamosus,* there is little change in estimates of M for different maximum ages.

Table 3.44. Intercept (a) and coefficient of regressions (b) of Catch Curve used to estimate total mortality of *Deania calceus* over the age estimate range. Standard error (S.E.) of the regression coefficient indicated along with sample size (n).

Sex	a	b	age groups	n	S.E.
male	9.799	-0.301	15 - 25	11	0.0659
female	8.319	-0.239	15 - 27	12	0.0295

Table 3.45. Total mortality (Z) with standard error, survivoirship (S), natural mortality (M) and fishing mortality (F) estimates for *Deania calceus*. Z and S estimated from catch curves of numbers at estimated age from long-line survey in December 1999. M derived from von Bertalanffy growth function using Pauly's (1980) relationship assuming mean ambient temperature to be 7^0C. F was determined by subtraction of M from Z. Estimates of M based on maximum age also given for *Centrophorus squamosus* and *Deania calceus*.

Species	Sex	Z	S	F	M	Method
Deania calceus	Male	0.301	0.74	0.124	0.177	Pauly, 1980
	Female	0.239	0.787	0.123	0.116	
Deania calceus	Male	0.301	0.74	0.142	0.159	
	Female	0.239	0.787	0.107	0.132	King, 1995 p 188-189
Centrophorus squamosus	Male				0.087	
	Female				0.066	

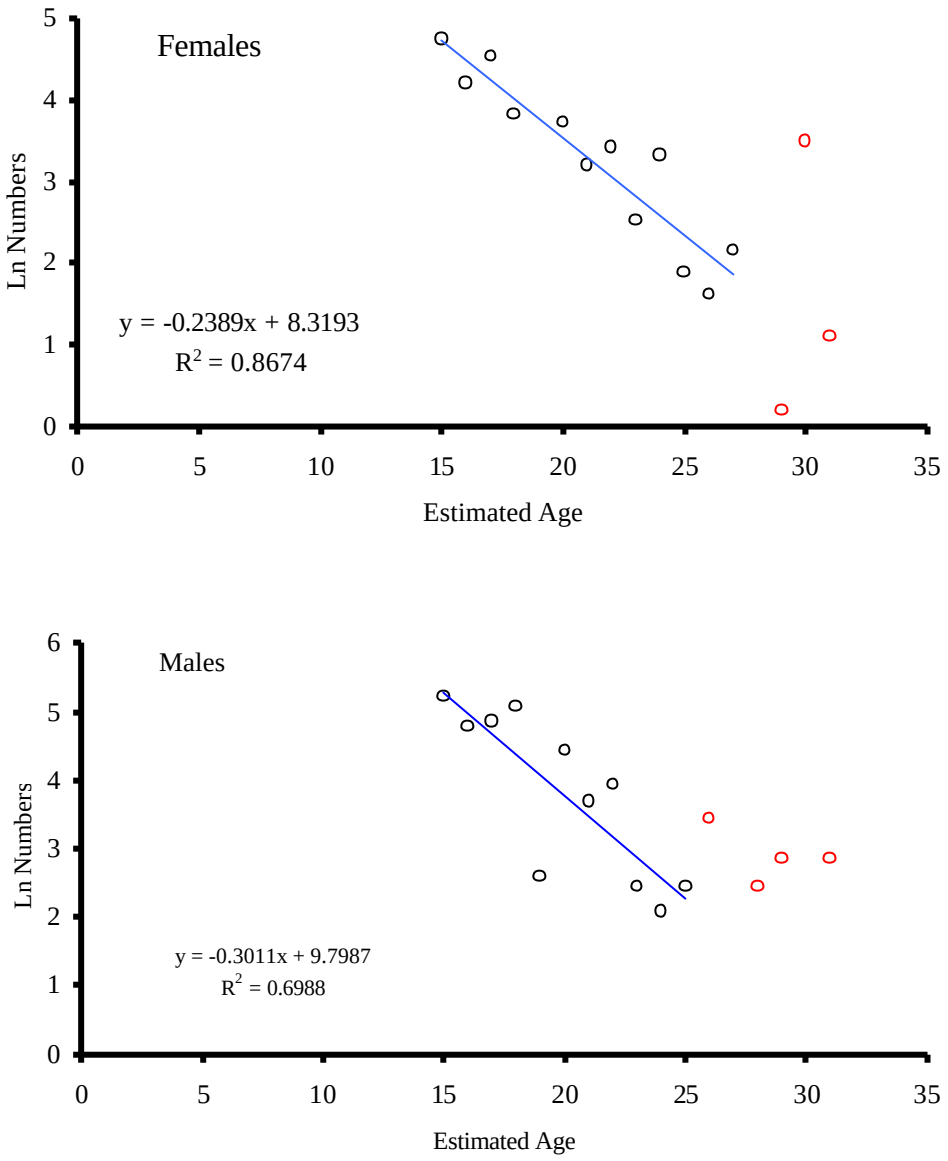

Fig. 3.69. Catch curves for male and female *Deania calceus* based on age estimation data from the entire study and catch numbers from December 1999 long-line survey of the slopes of the Porcupine Bank. Red indicates estimated age groups not included in the analysis

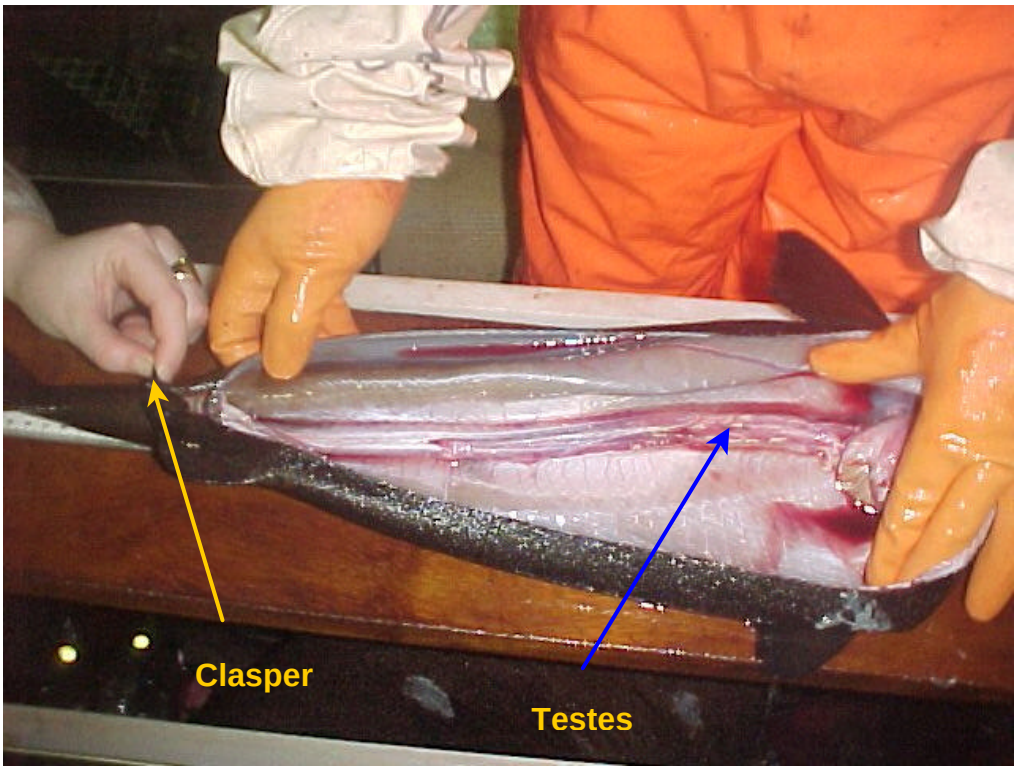

Plate 3.1. Dissection of maturity stage 1 *Centroscymnus coelolepis* male showing tiny claspers and testes.

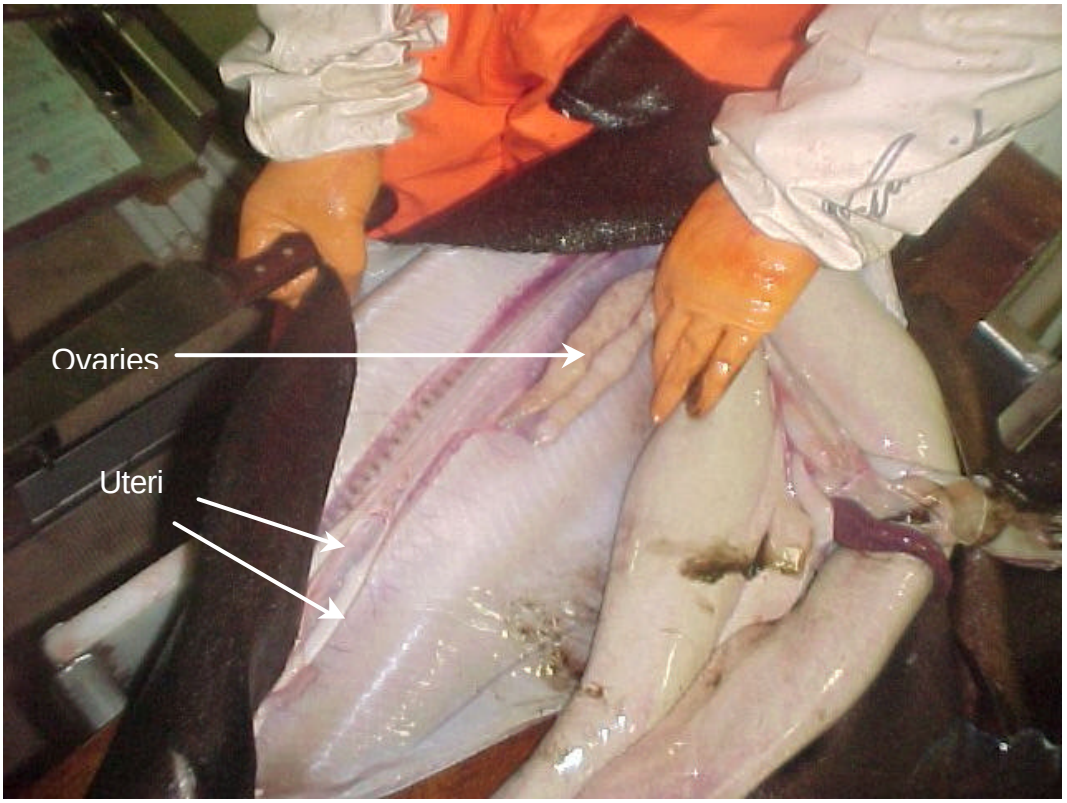

Plate 3.2. Dissection of maturity stage 1 *Centroscymnus coelolepis* female showing ovaries and uteri.

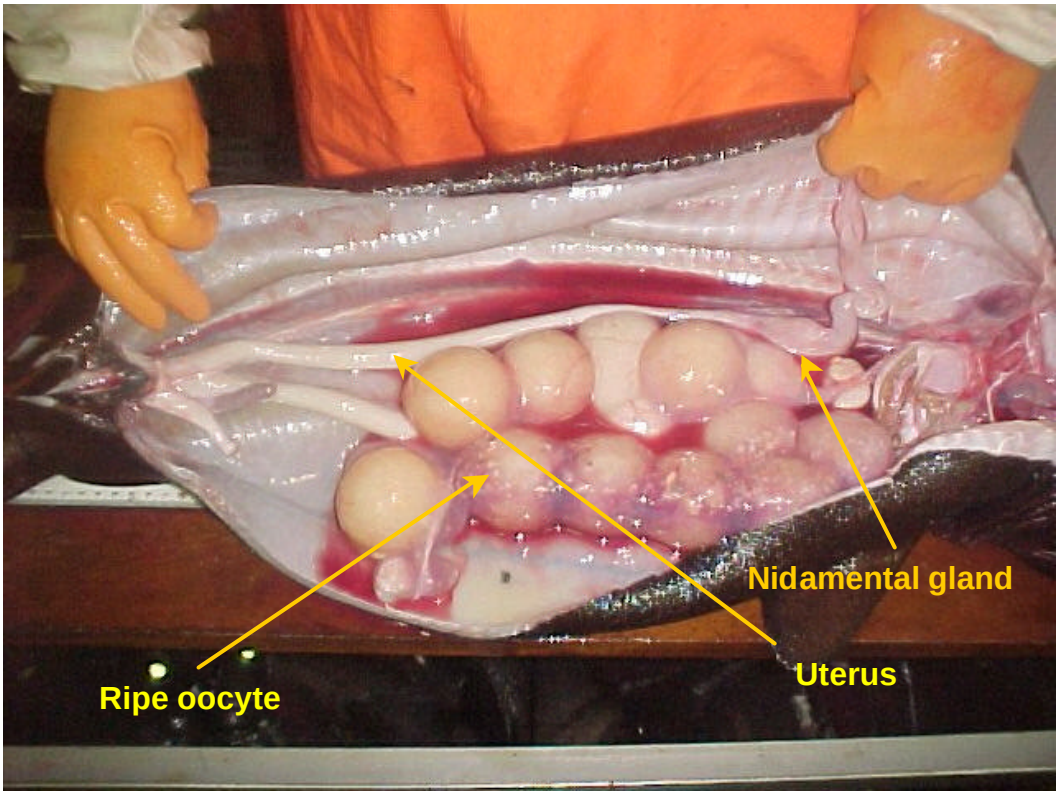

Plate 3.3. Dissection of maturity stage 3 *Centroscymnus coelolepis* female showing ripe ovarian oocytes, nidamental gland and uteri.

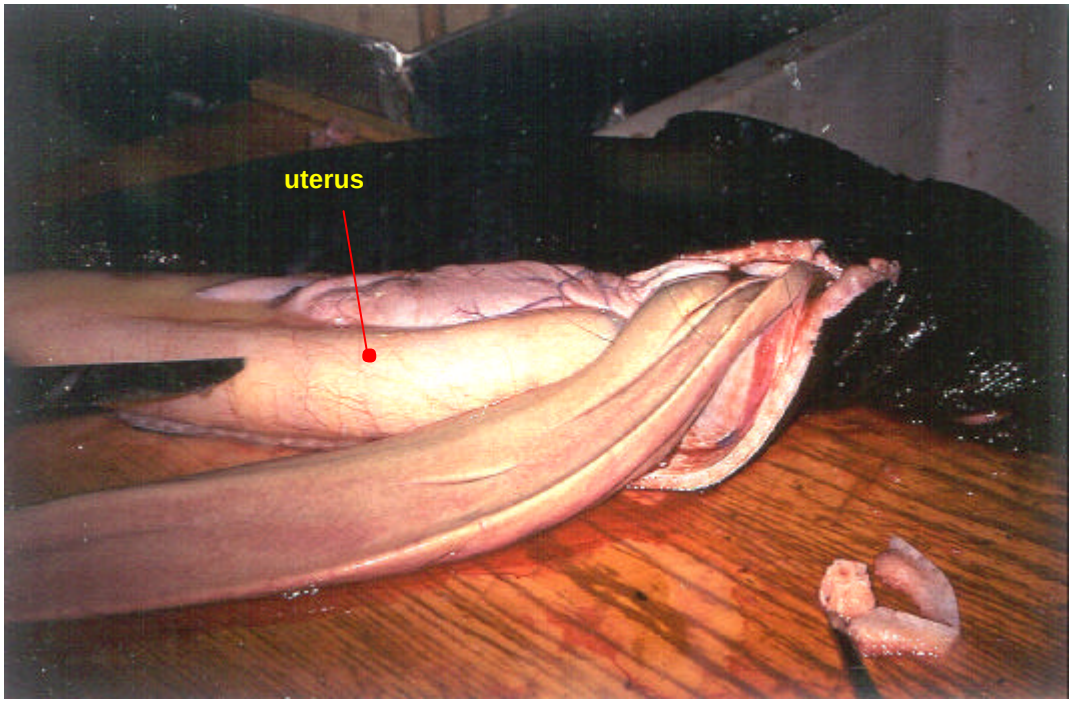

Plate 3.4. Dissection of stage 4 female *Centroscymnus coelolepis* showing the "candled" uteri containing undifferentiated yolk. The ovaries are much reduced in size and contain only small oocytes.

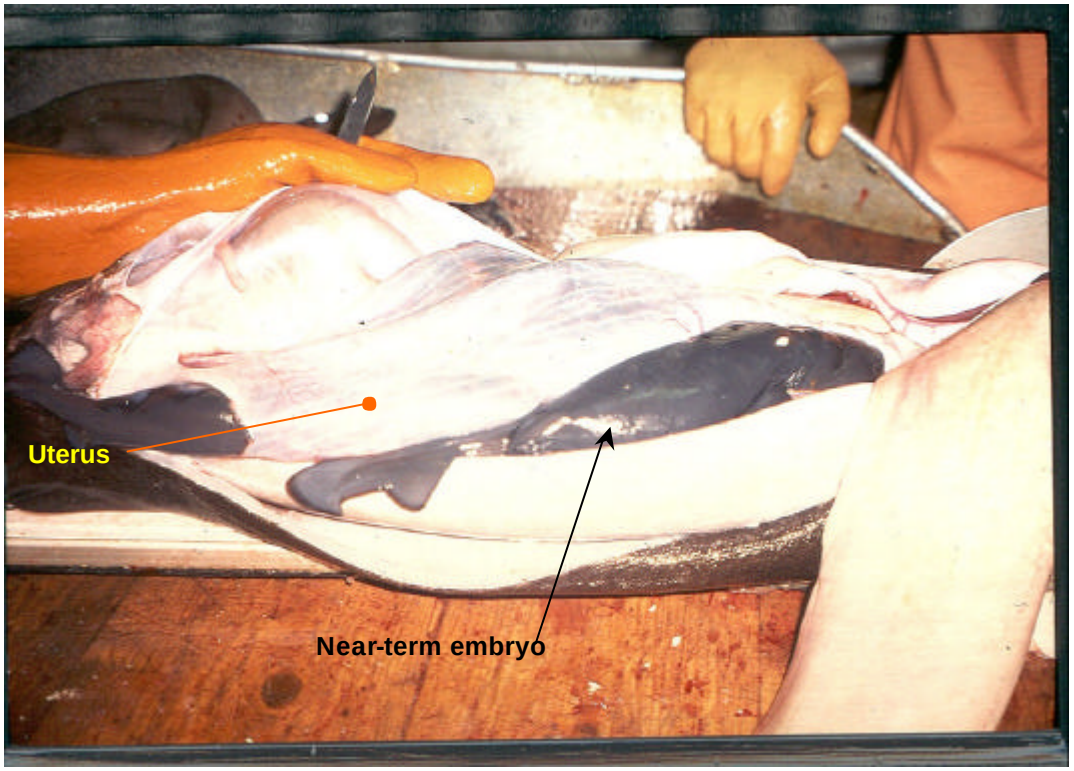

Plate 3.5. Dissection of stage 6 female *Centroscymnus coelolepis*, both uteri contain near-term embryos.

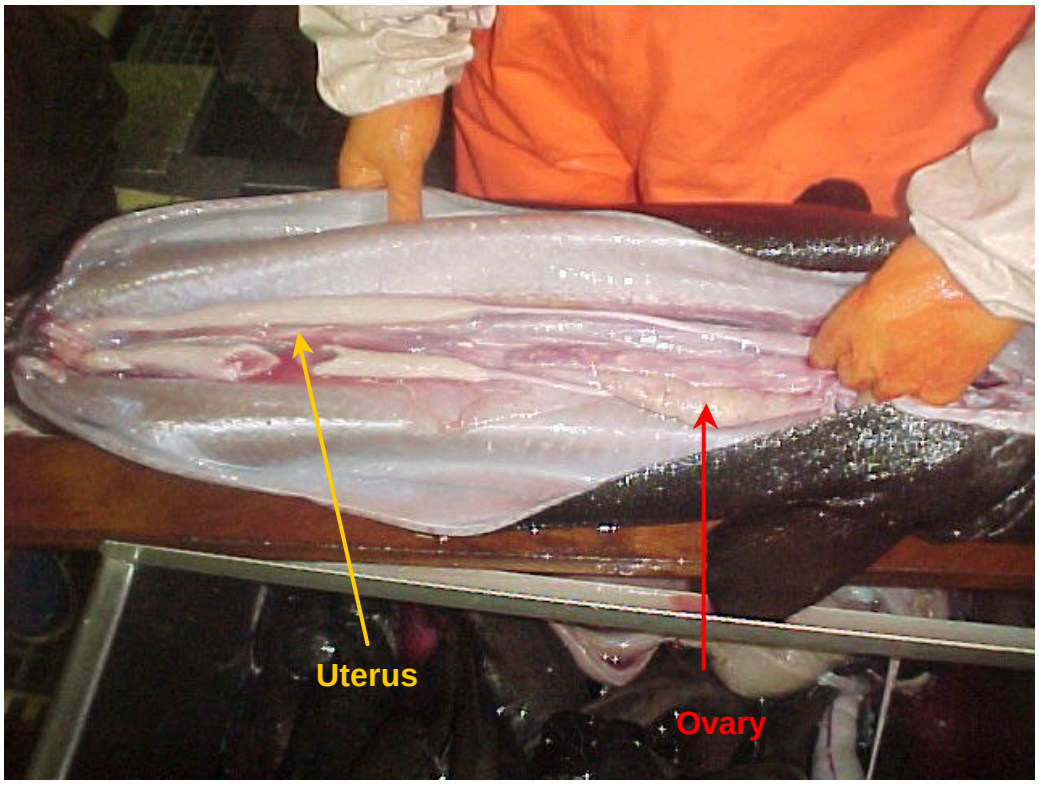

Plate 3.6. Dissection of maturity stage 7 *Centroscymnus coelolepis* female showing dilated uteri and ovary.

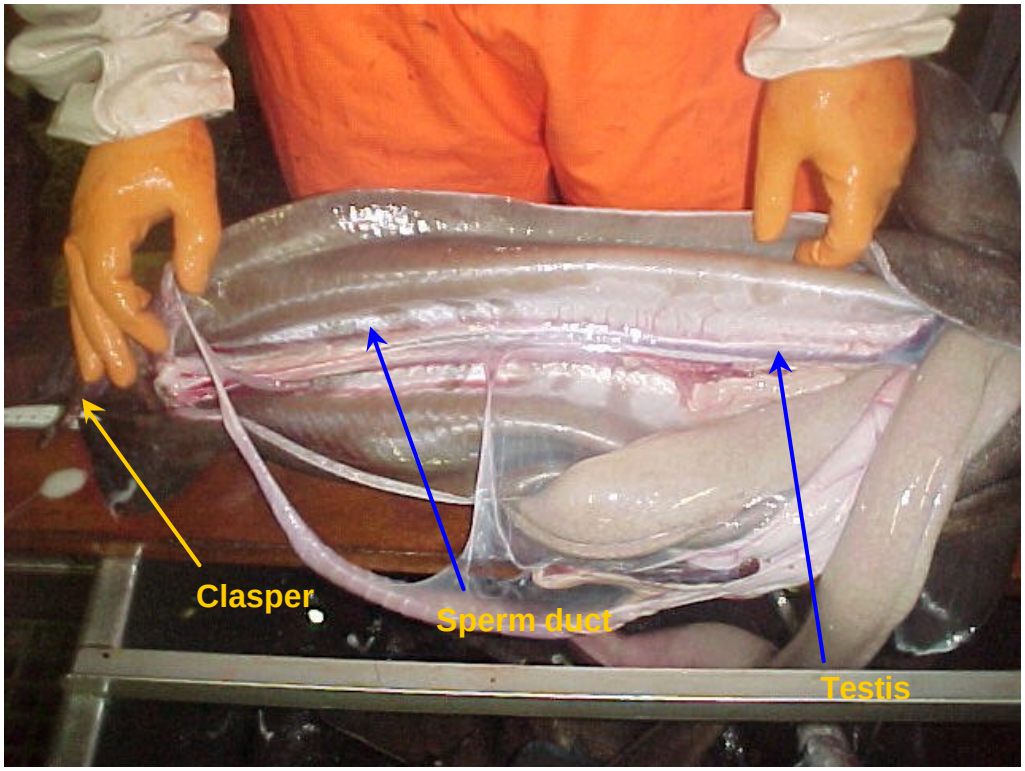

Plate 3.7. Dissection of maturity stage 2 *Centrophorus squamosus* male showing flexible claspers, developing testes and meandering sperm ducts.

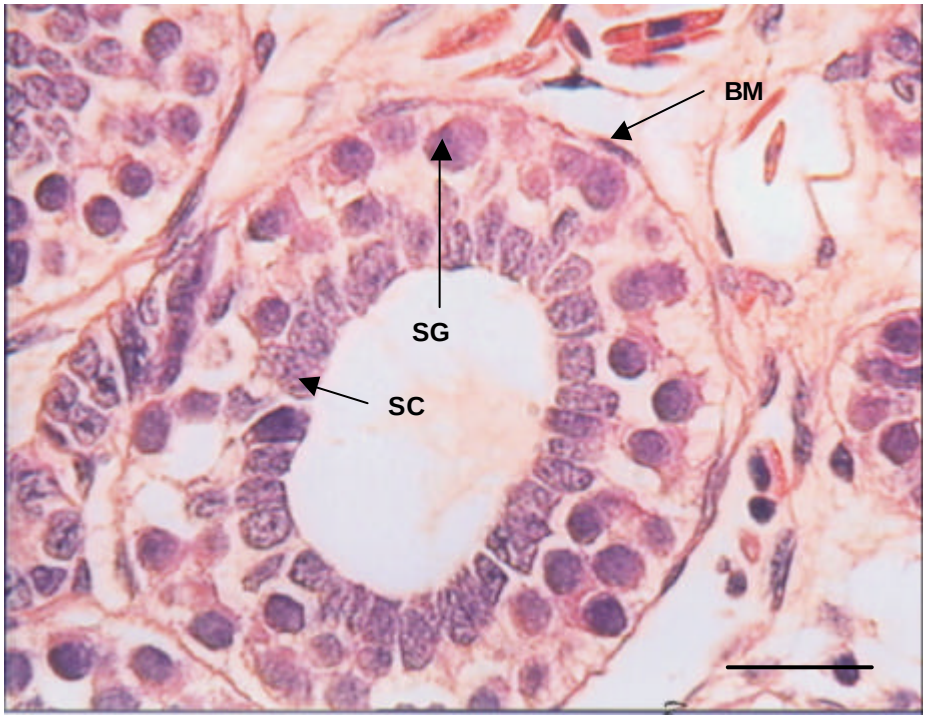

Plate 3.8. Spermatocyst containing spermatogonia in *Deania calceus*, x 40. Sertoli cells (SC) towards lumen and spermatogonia (SG) towards basement membrane (BM). Scale bar: 50 µm.

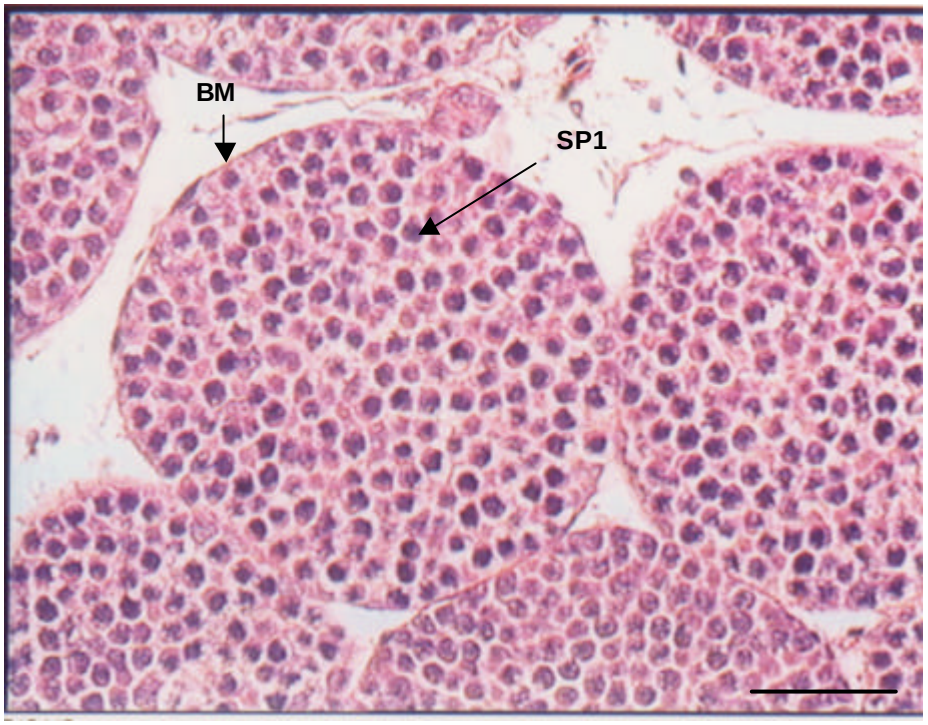

Plate 3.9. Spermatocysts containing basophilic primary spermatocytes (SP1), basement membrane (BM) clearly evident *Deania calceus* x 20. Scale bar: 100 µm.

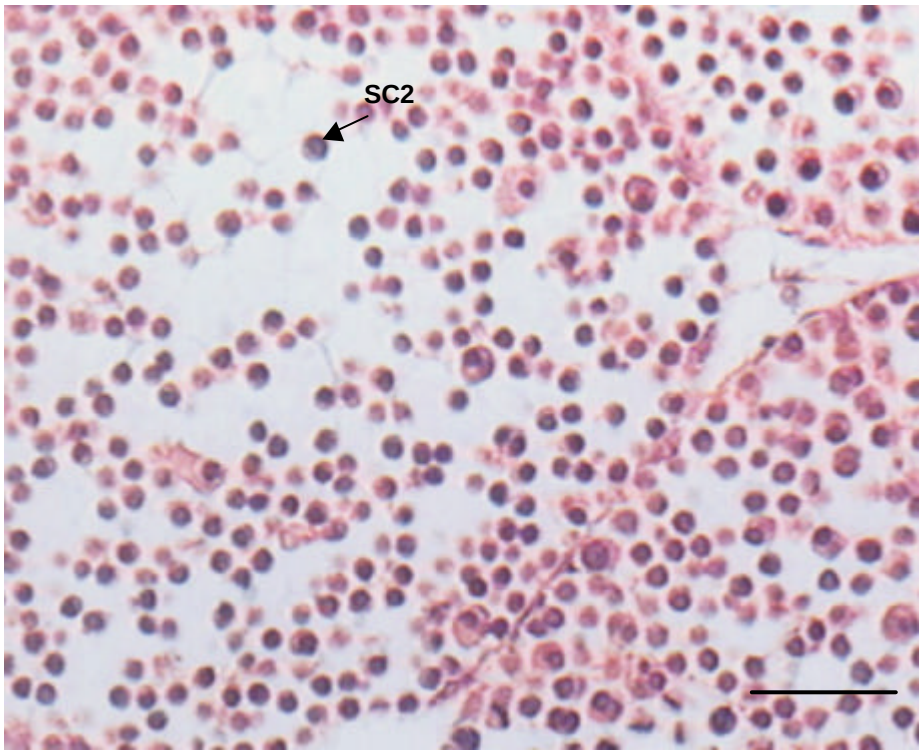

Plate 3.10. Spermatocysts containing secondary spermatocytes, *Deania calceus* x 40. Nuclei of secondary spermatocytes (SC2) tiny. Scale bar: 50 µm.

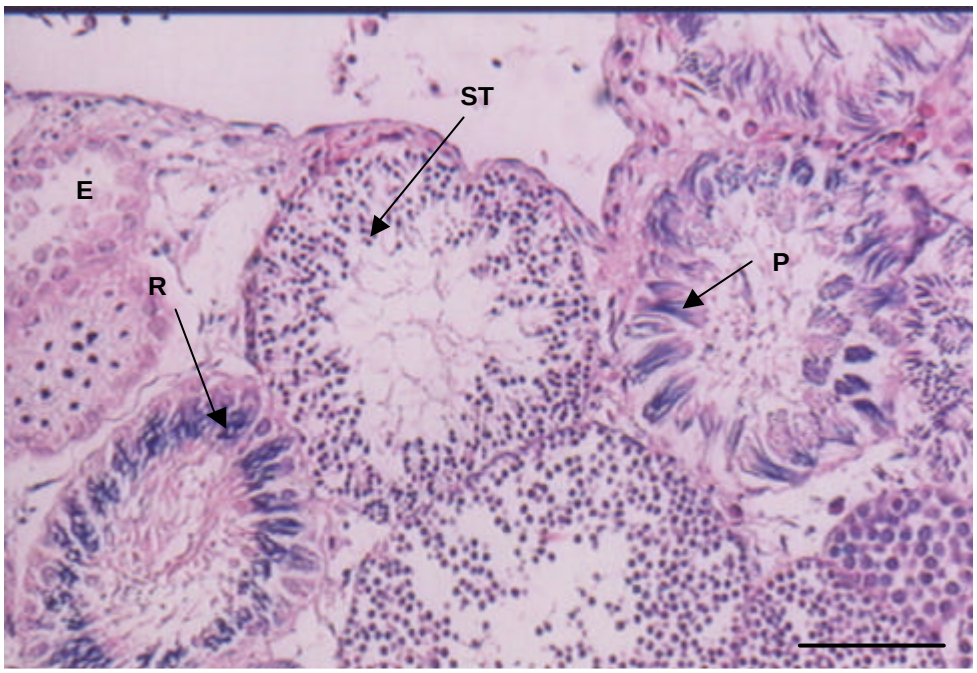

Plate. 3.11. Various stages of spermatogenesis in *Deania calceus* x 20 Centre of picture spermatocyst containing spermatids (ST) with elliptical nuclei. To right spermatozoans arranged in parallel (P) and to left spermatozoa in coiled arrangement (R) and evacuated spermatocysts (E). Scale bar: 100 µm.

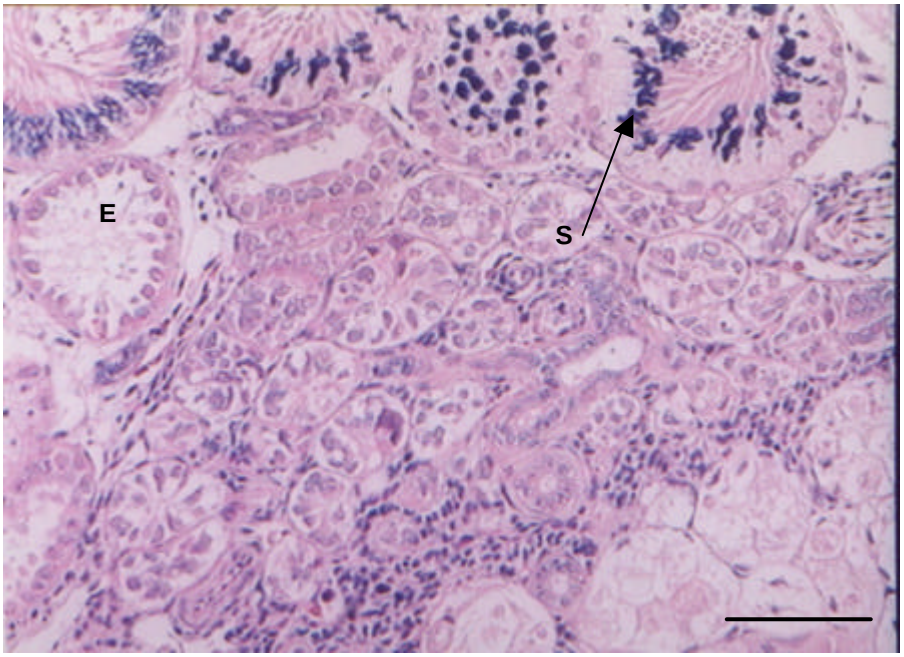

Plate 3.12. Spermatocysts with ripe spermatozoa (S) and evacuated spermatocysts (E) with remnants of Sertoli cells *Deania calceus* x 20. Scale bar: 100 µm.

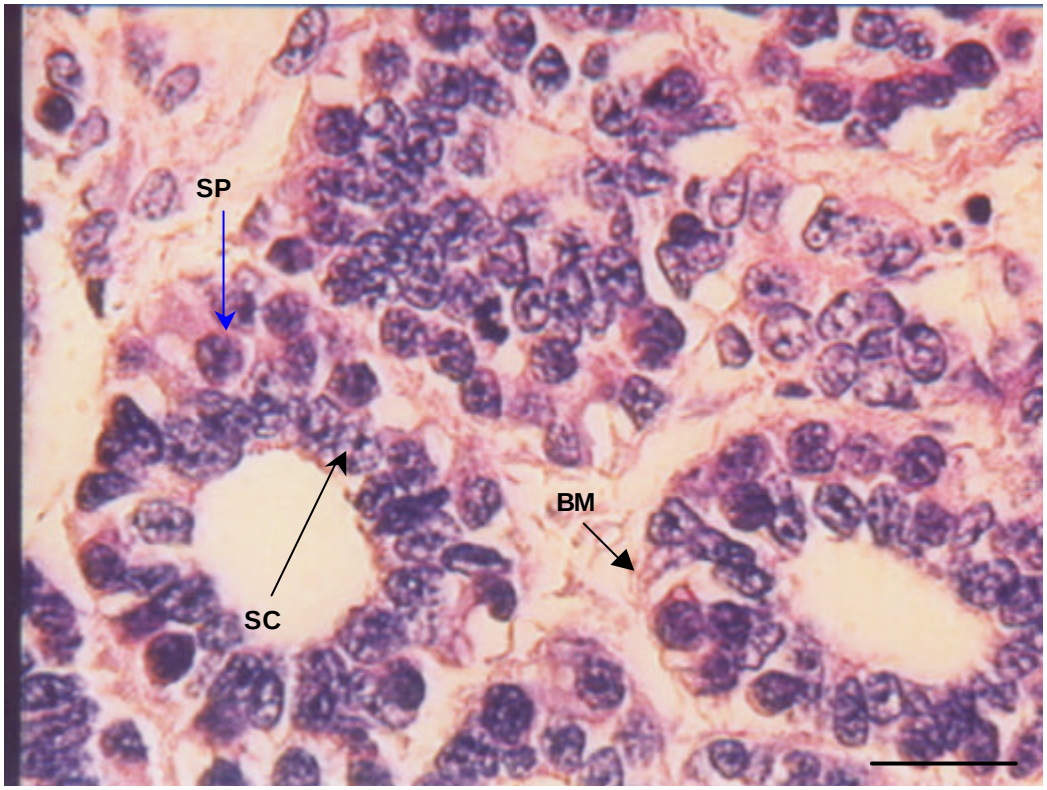

Plate 3.13. Spermatocysts containing spermatogonia in *Centroscymnus coelolepis testis* x 40 the Sertoli cells (SC) are arranged around the lumen with the spherical spermatogonial (SP) nuclei towards the basement membrane (BM). Scale bar: 50 µm.

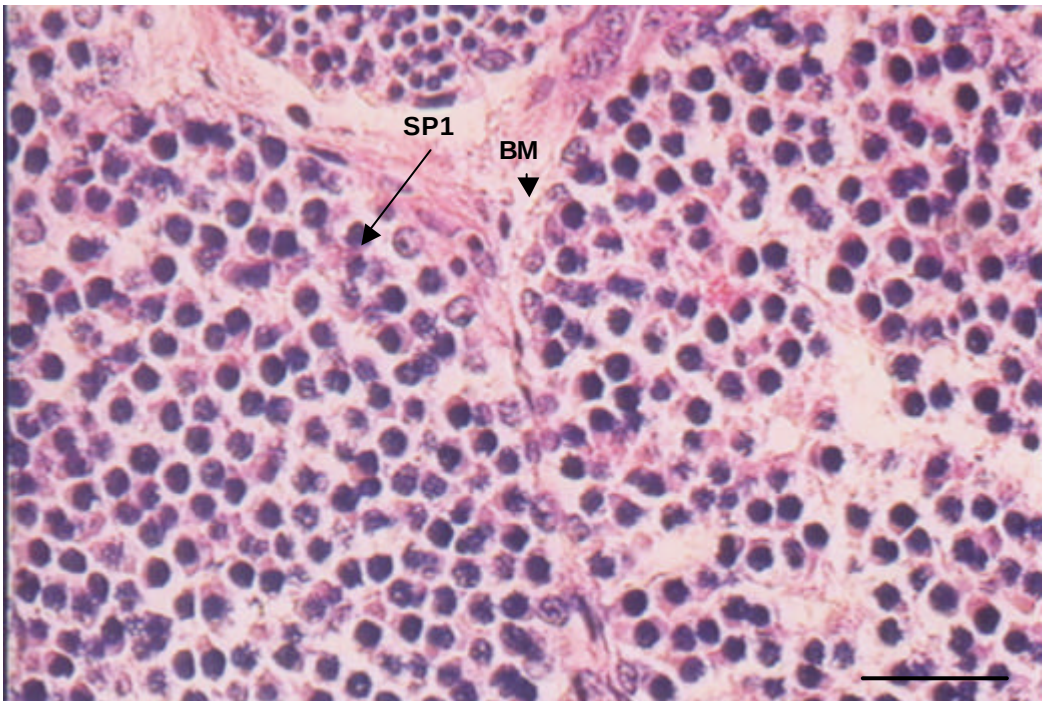

Plate 3.14. Spermatocysts containing primary spermatocytes in *Centroscymnus coelolepis* testis x 40. Basophilic primary spermatocyte nuclei (SP1) clearly evident. Spermatocysts distinguishable by basement membrane (BM). Scale bar: 50 µm.

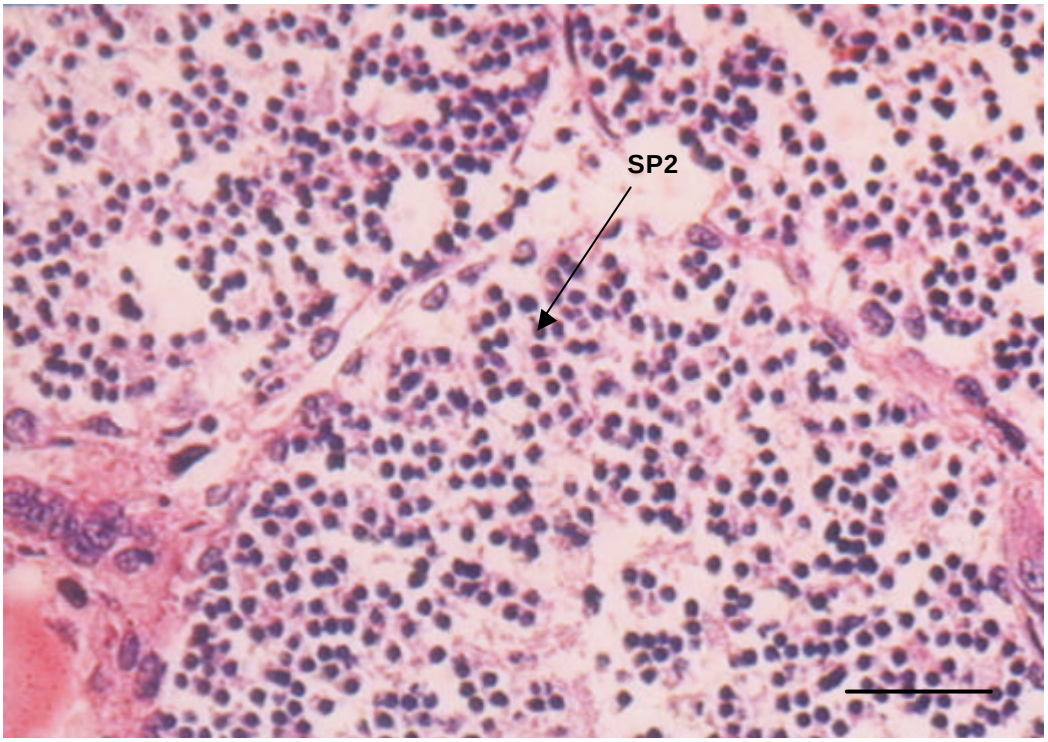

Plate 3.15. Spermatocysts containing secondary spermatocytes in testis of *Centroscymnus coelolepis*, x 20. Secondary spermatocyte (SP2) nuclei are tiny and densely basophilic. Scale bar: 100 µm.

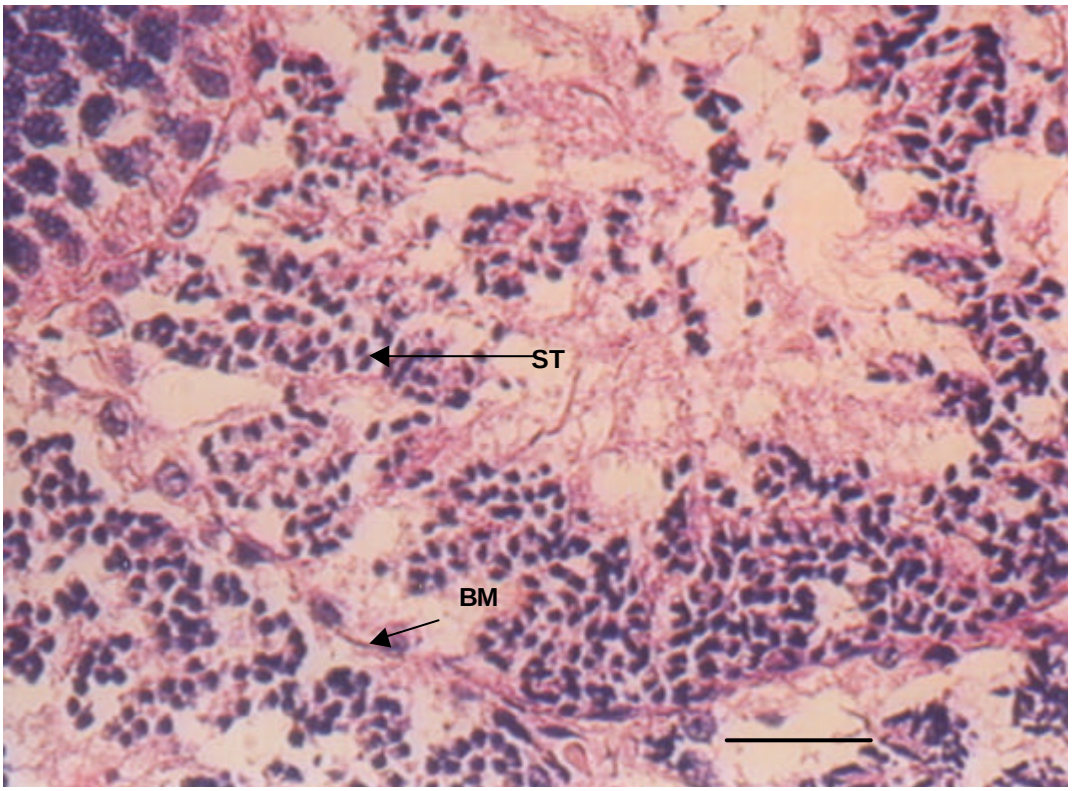

Plate 3.16. Spermatocysts containing spermatids, *Centroscymnus coelolepis*, x 20. Spermatids (ST) with elliptical nuclei, Sertoli cells along basement membrane (BM). Scale bar: 100 µm.

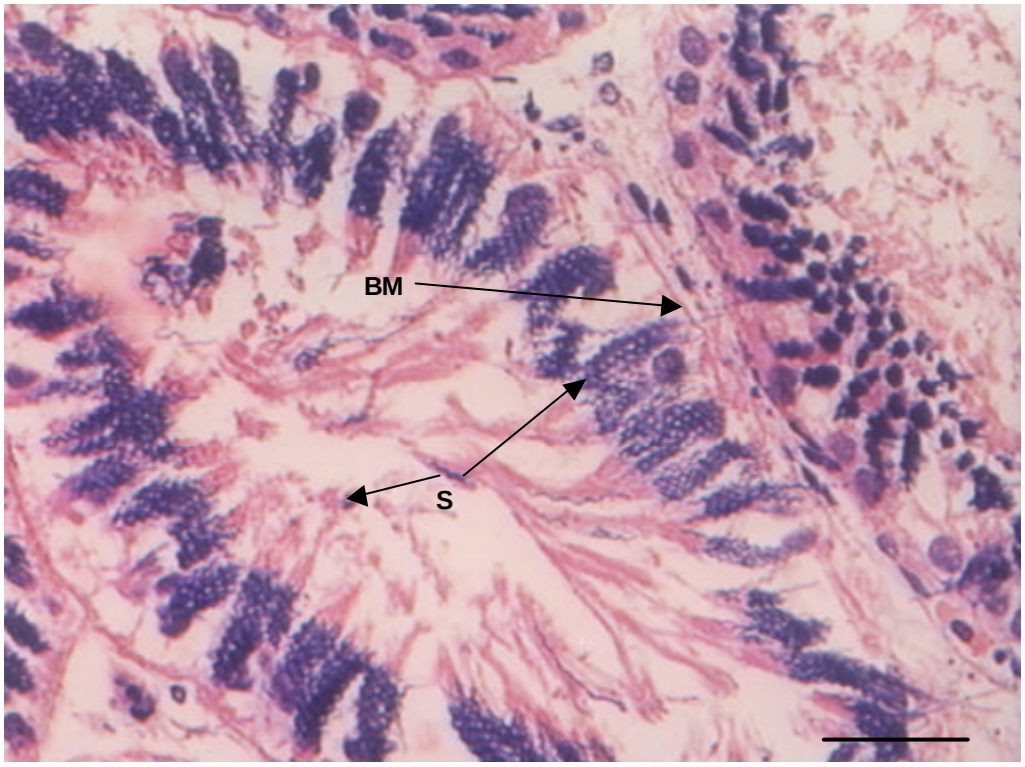

Plate 3.17. Spermatocyst containing ripe spermatozoa, *Centroscymnus coelolepis*, x 20. Clusters of ripe spermatozoa (S) have their helical heads towards basement membrane (BM). Tails towards the lumen. Scale bar: 100 µm.

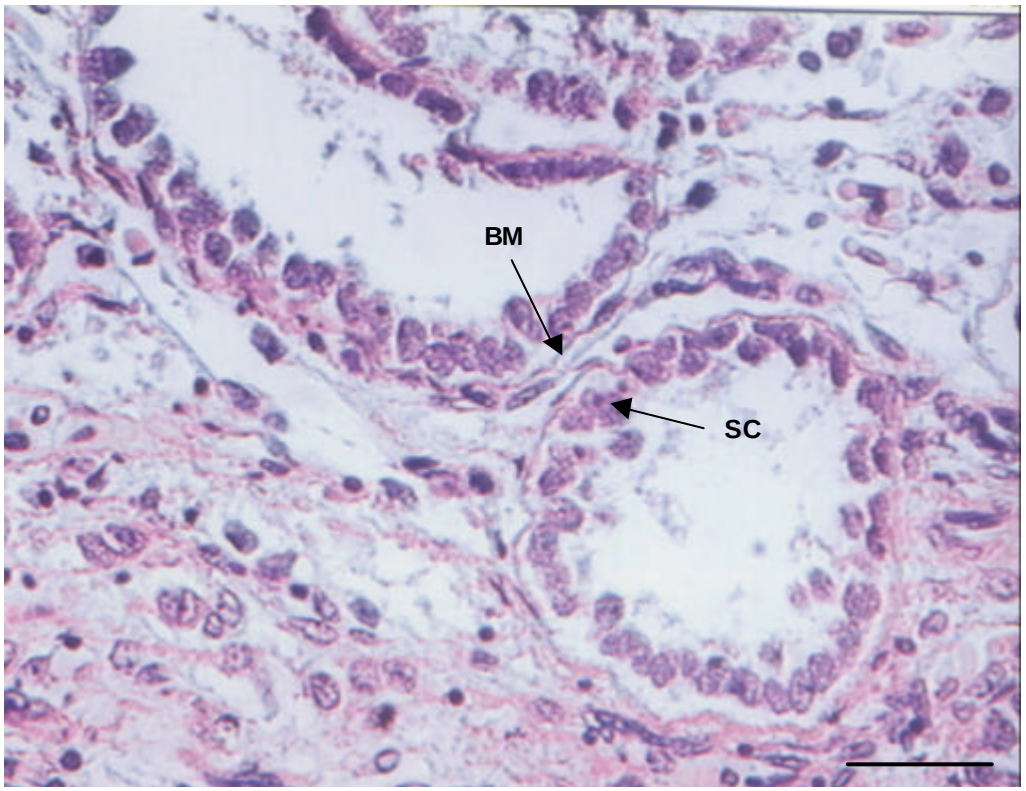

Plate 3.18. Evacuated spermatocysts defined by basement membrane (BM) containing remnants of Sertoli cells (SC) in the testis of *Centroscymnus coelolepis*, x 20. Scale bar: 100 µm.

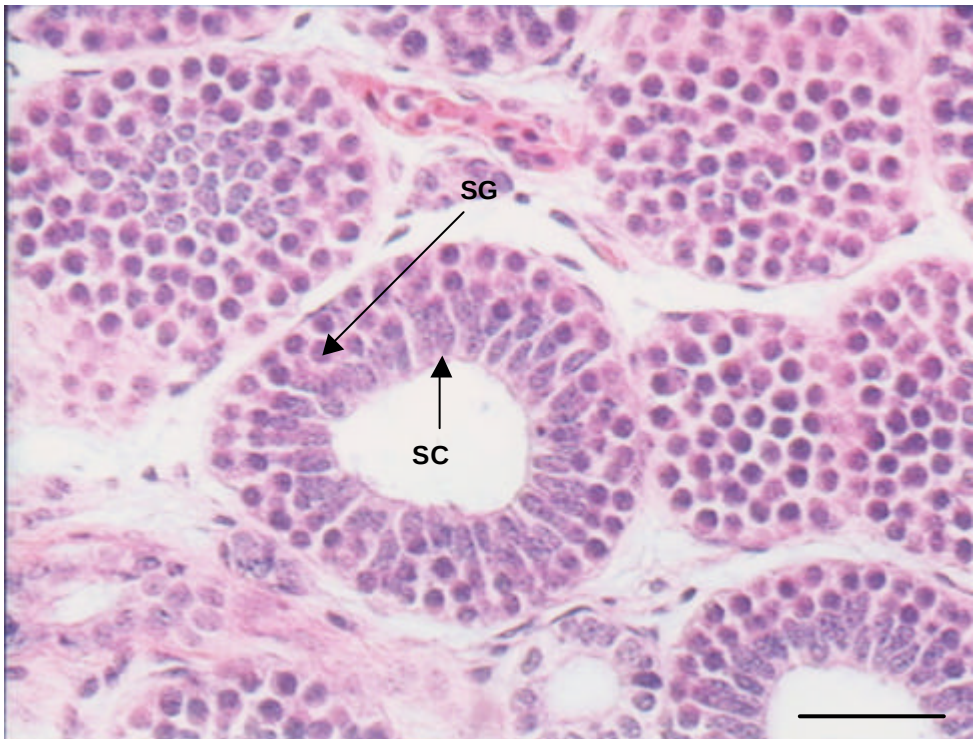

Plate 3.19. Spermatocyst containing spermatogonia (SG) and Sertoli cells (SC), x 20 *Centrophorus squamosus*. Scale bar: 100 µm.

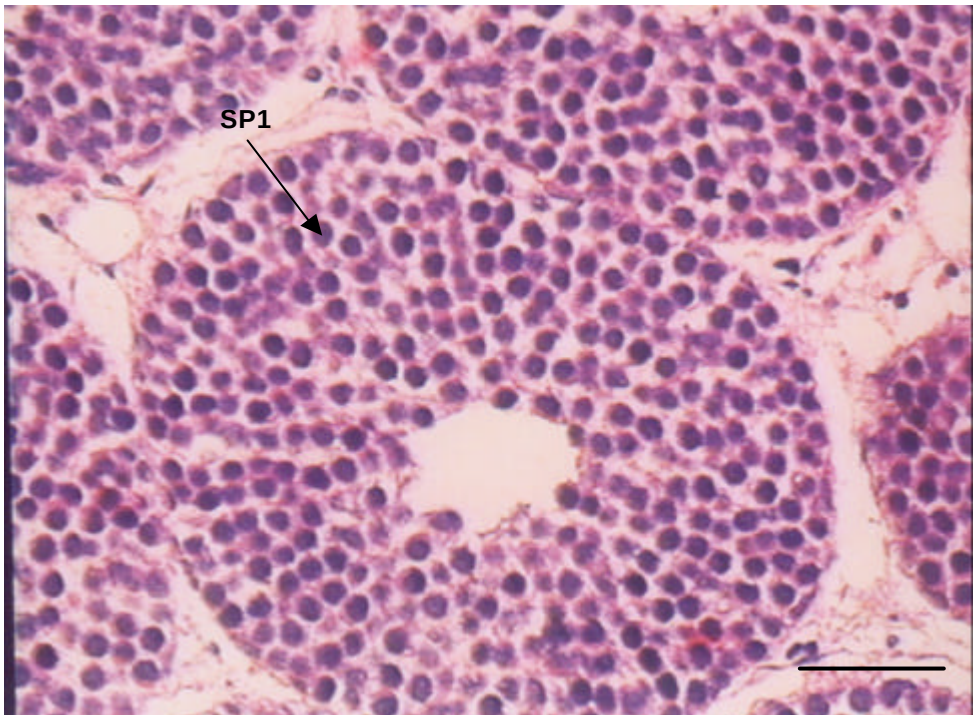

Plate 3.20. Spermatocyst containing primary spermatocytes (SP1) with basophilic nuclei, x 20 *Centrophorus squamosus*. Scale bar: 100 µm.

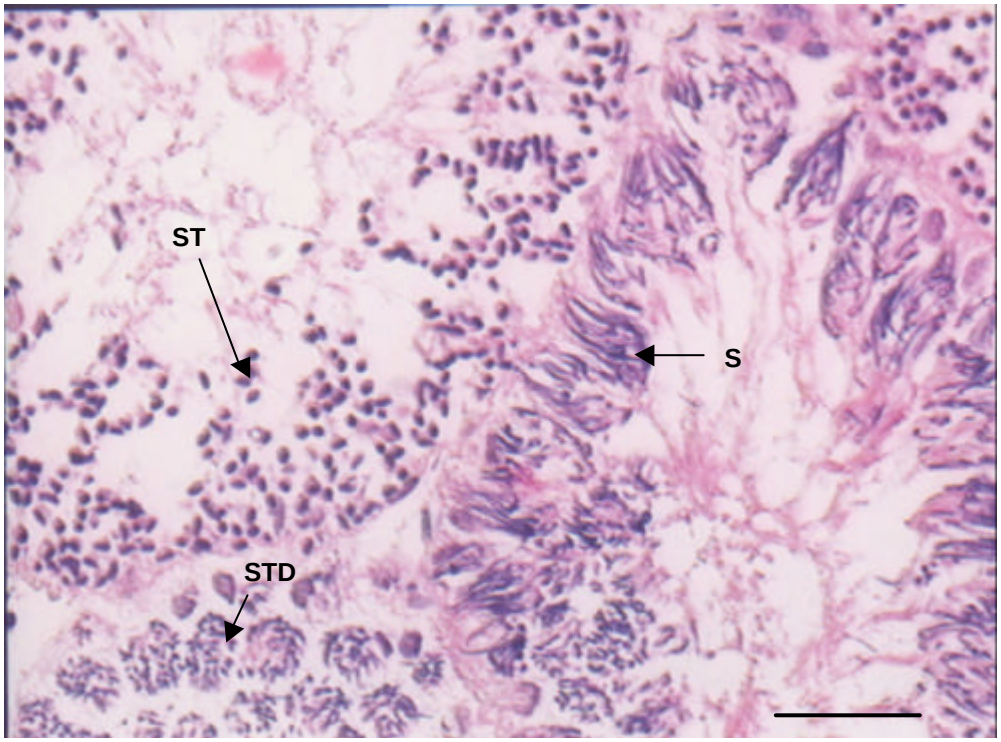

Plate 3.21. Spermatocysts containing spermatids (ST) and in a more advanced state of development (STD) and spermatozoa with heads arranged in parallel (S) x 20, *Centrophorus squamosus*. Scale bar: 100 µm.

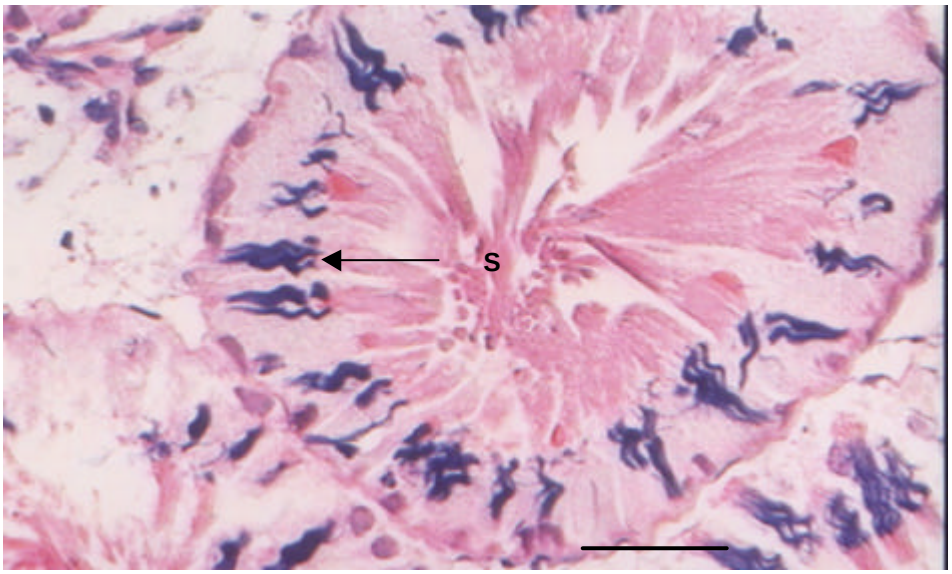

Plate 3.22. Spermatocyst containing clumps of ripe spermatozoa (S), *Centrophorus squamosus*, x 20. Scale bar: 100 µm.

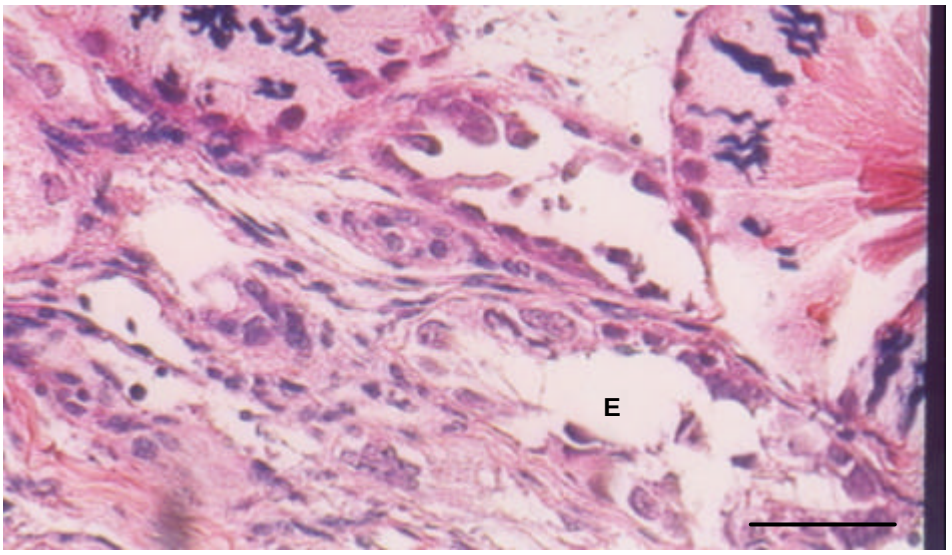

Plate 3.23. Evacuated spermatocysts (E), *Centrophorus squamosus* x 20. Scale bar: 100 µm.

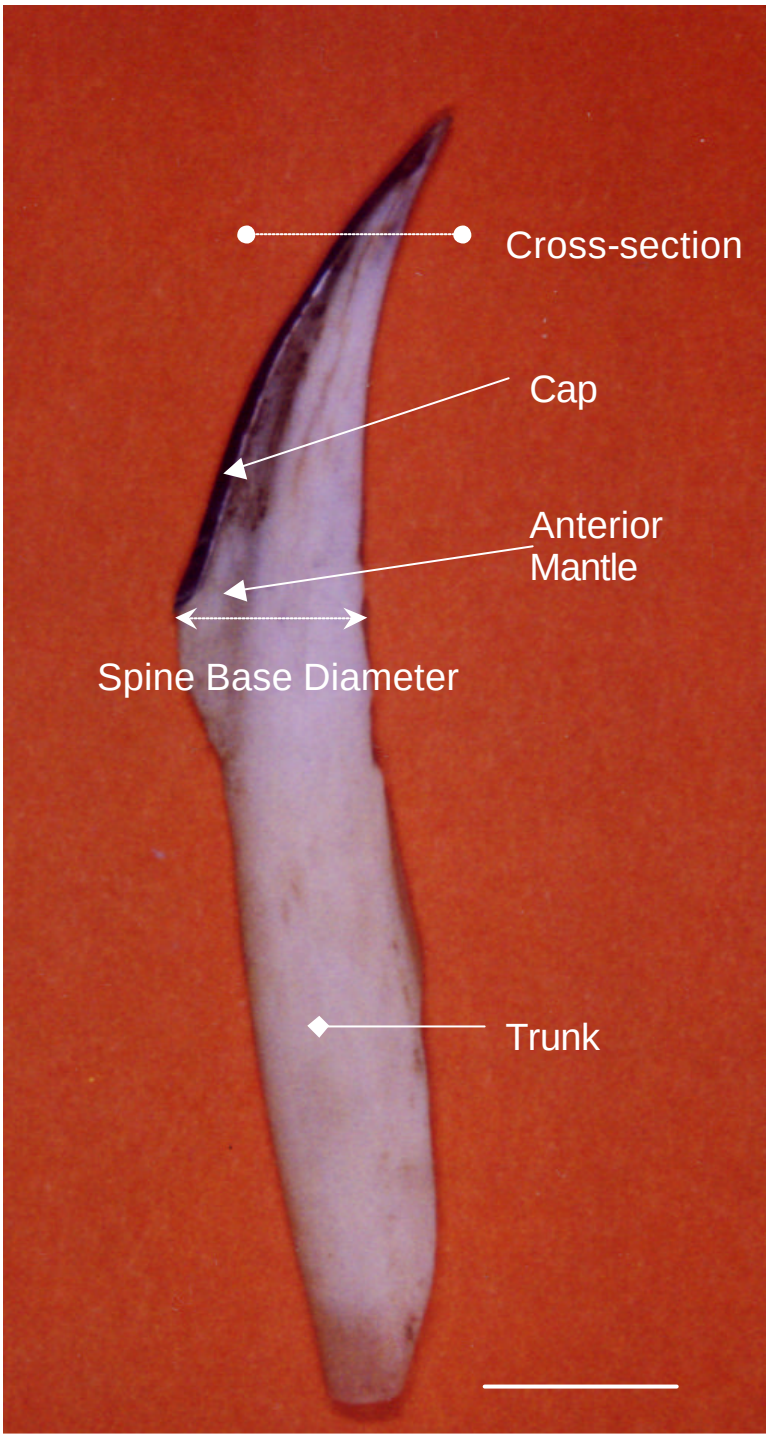

Plate 3.24. First dorsal spine of *Centrophorus squamosus* showing external features and position of cross-sections. Scale bar indicates 100 mm.

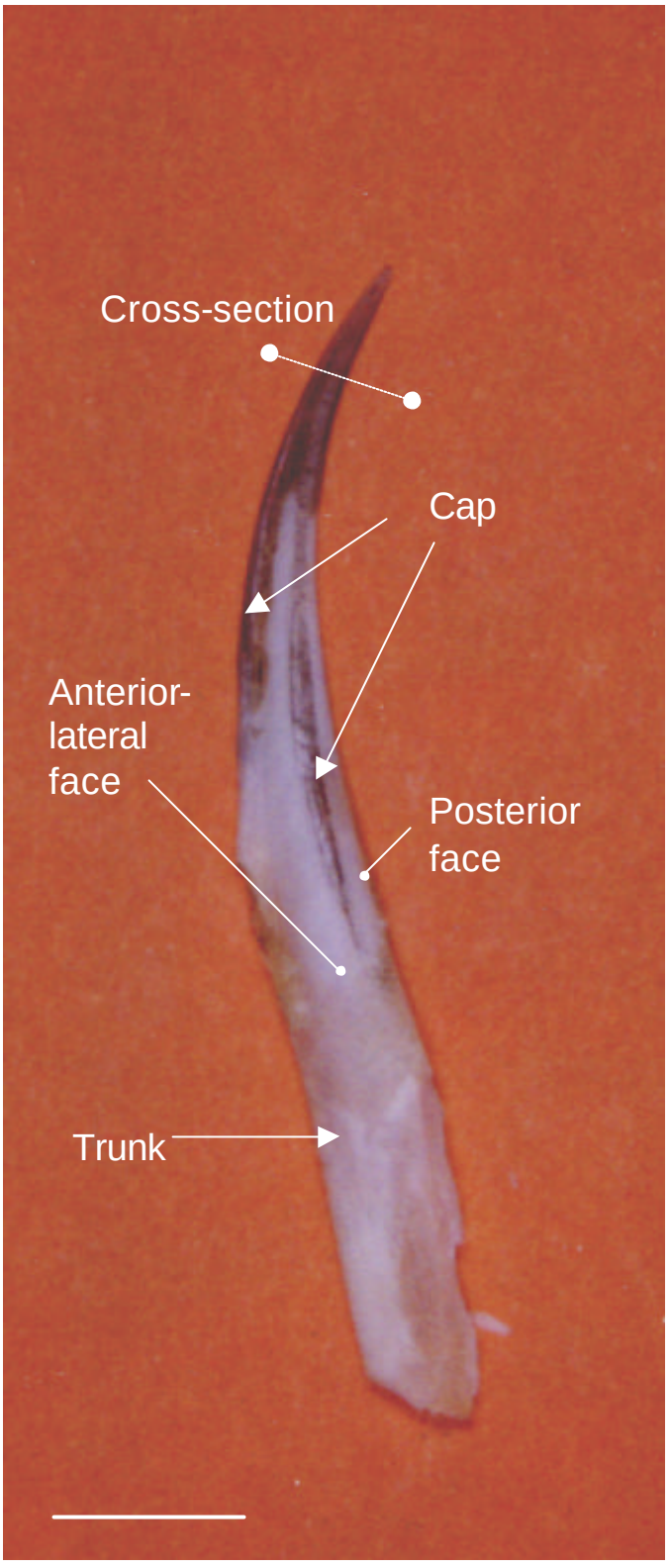

Plate 3.25. Second dorsal spine of *Deania calcea* showing surface morphology and position of cross-section from which age estimates were obtained. Scale bar indicates 100 mm.

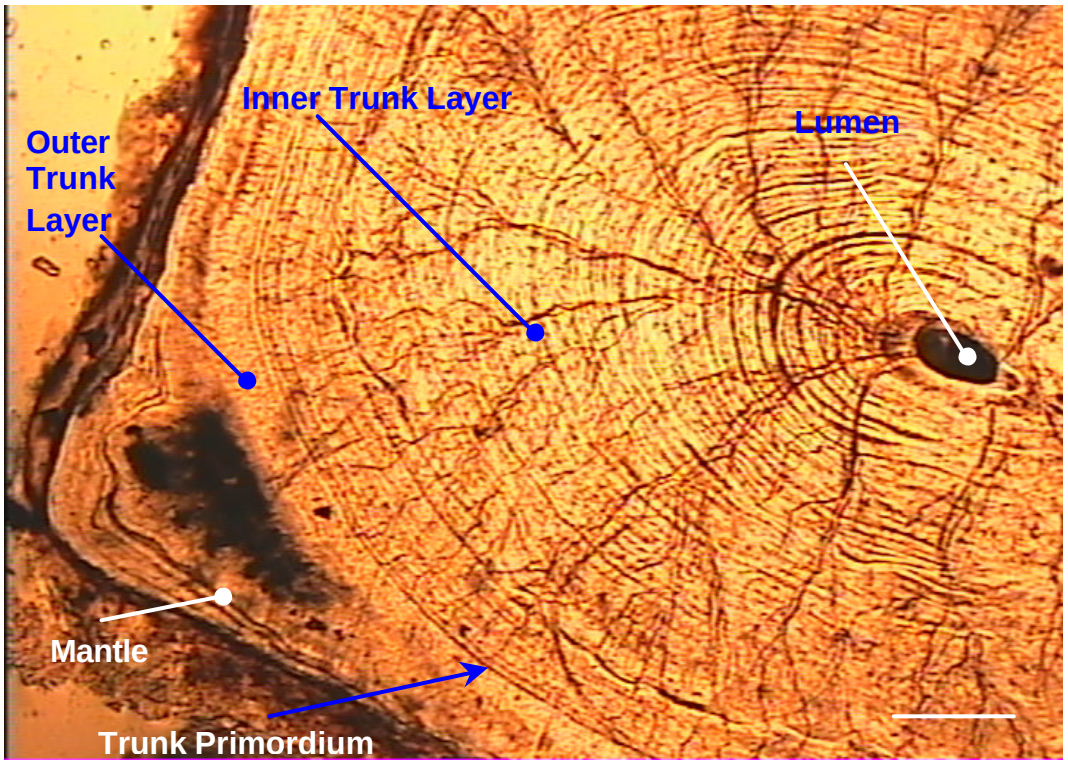

Plate 3.26. Section of second dorsal spine of a 97 cm TL female (x40) specimen of *Centrophorus squamosus*, of estimated age 43 years, caught on 4th August 1997 in the Rockall Trough. Bar: 500 µm.

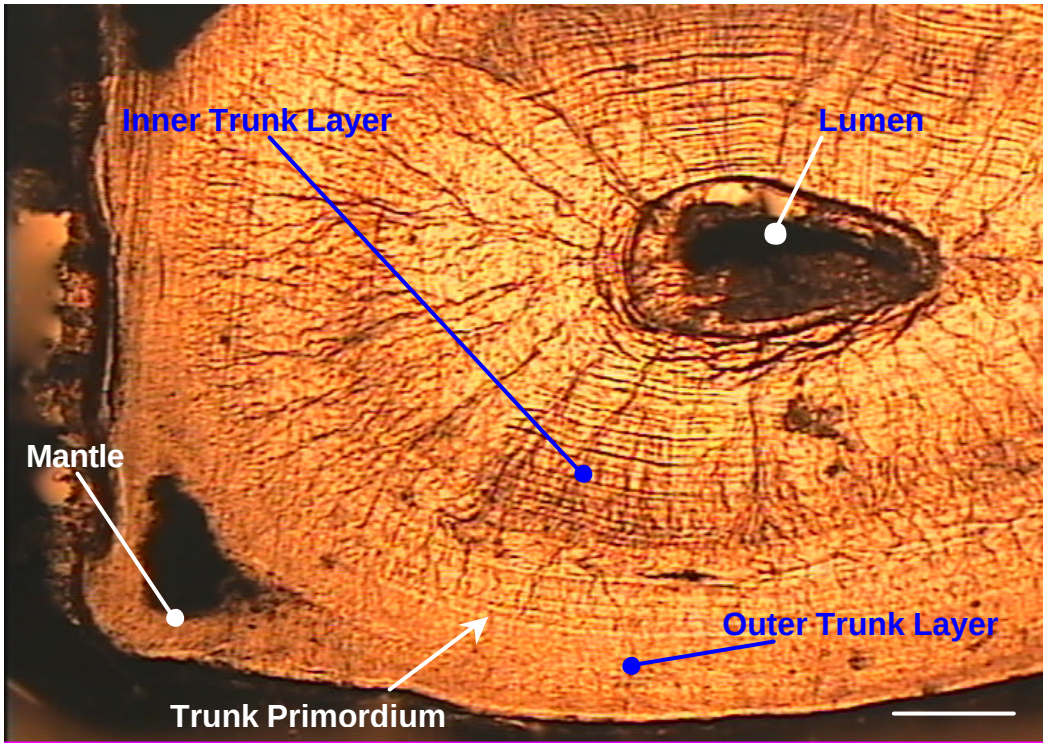

Plate.3.27. Section of 1st dorsal spine (x40) of a 99 cm TL male specimen of *Centrophorus squamosus*, of estimated age 39 years, caught on the 31st October 1997 in the Rockall Trough. Bar: 500 µm.

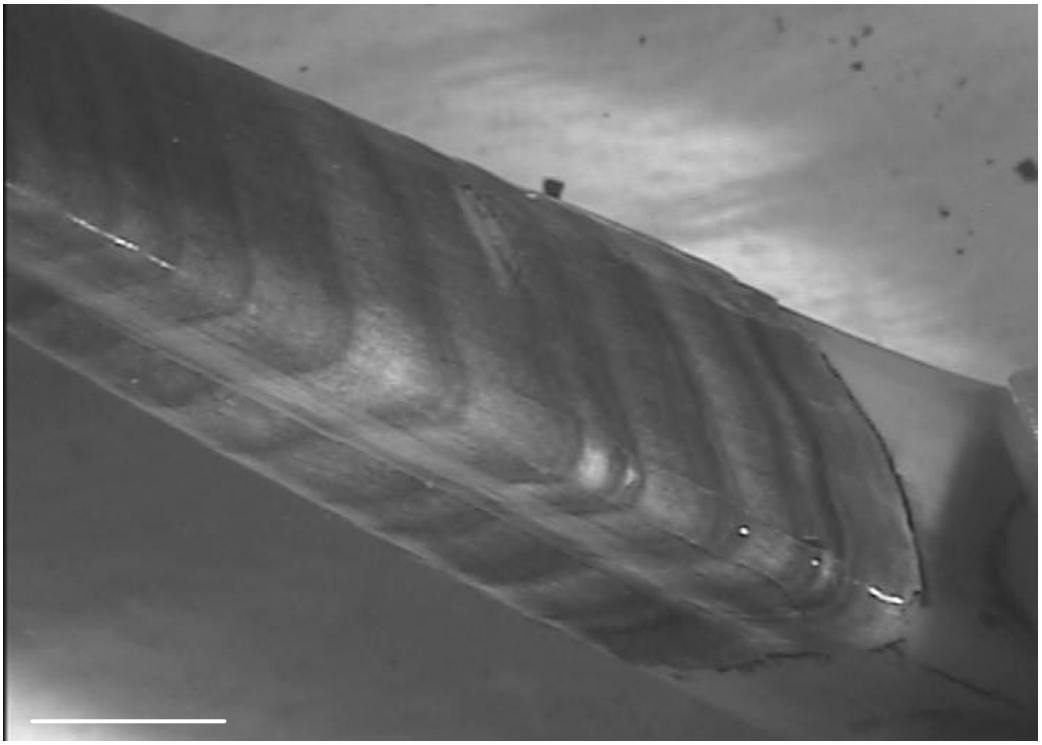

Plate 3.28. Photomicrograph (x5) of *Squalus. acanthias* 2nd dorsal spine base with visible annuli on enamel cap. Scale bar: 250 µm.

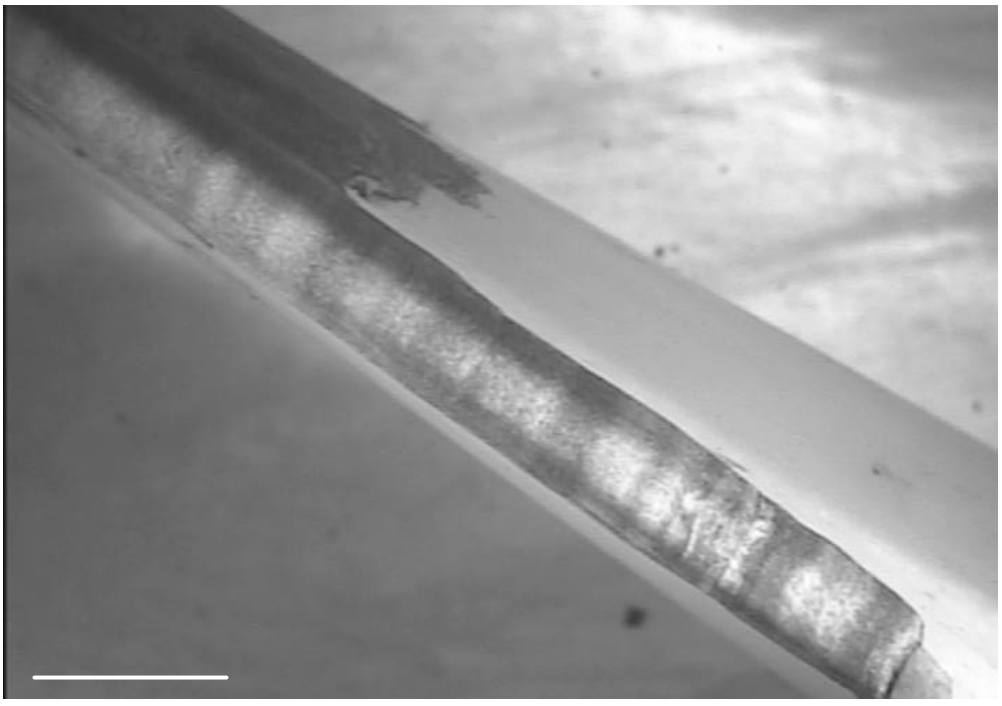

Plate 3.29. Photomicrograph (x 5) of 2nd dorsal spine of *Centrophorus squamosus* spine base with marks visible on the enamel of the cap. Scale bar: 250 µm.

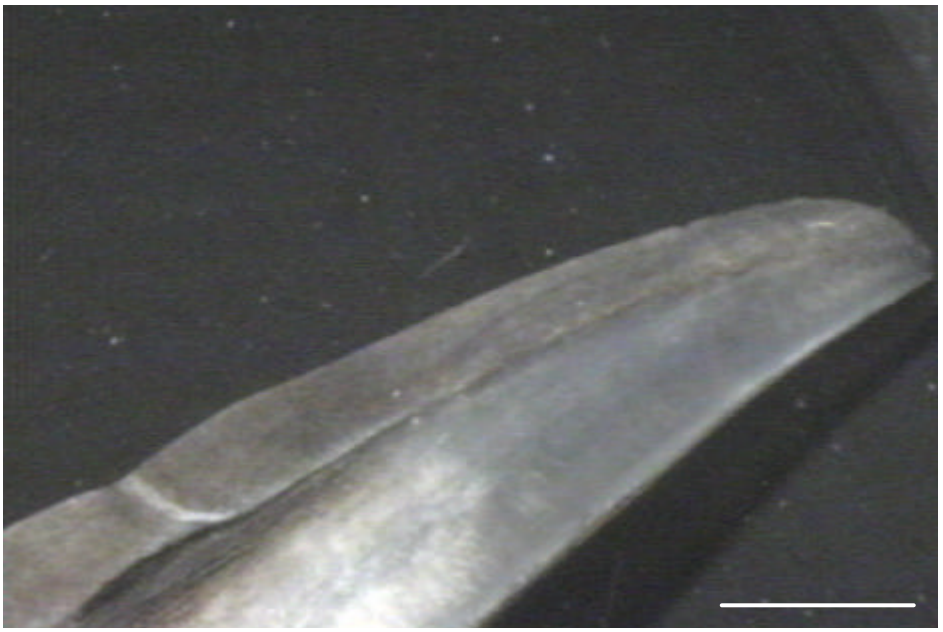

Plate 3.30. Tip of spine of *Centrophorus squamosus* x 5 showing clear white mark, possible associated with parturition. Scale bar: 250 µm.

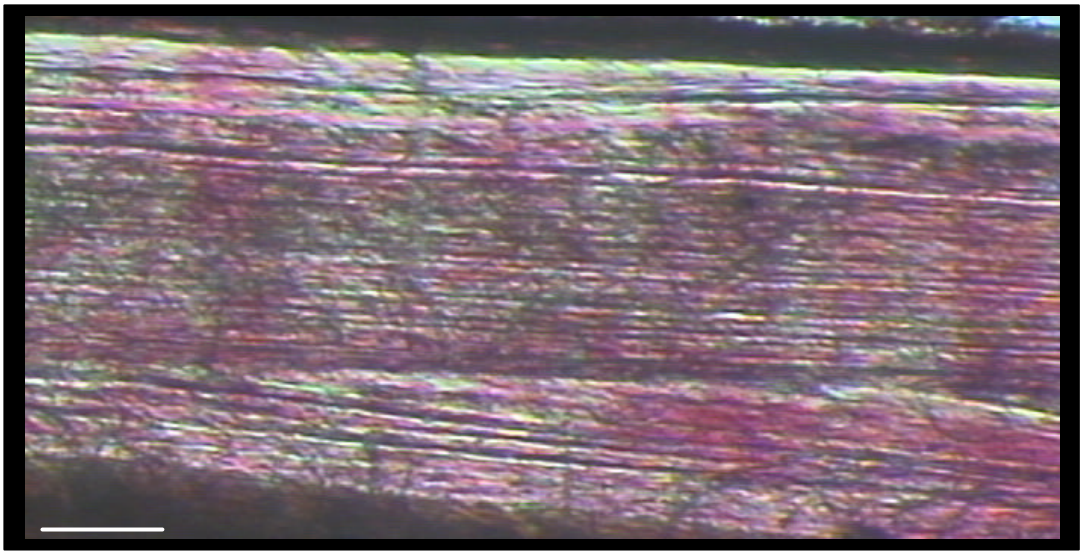

Plate 3.31. Transverse section of spine of *Centrophorus squamosus* x 40, the inner dentine zones appear to converge proximally (to the left). Scale bar: 500 µm.

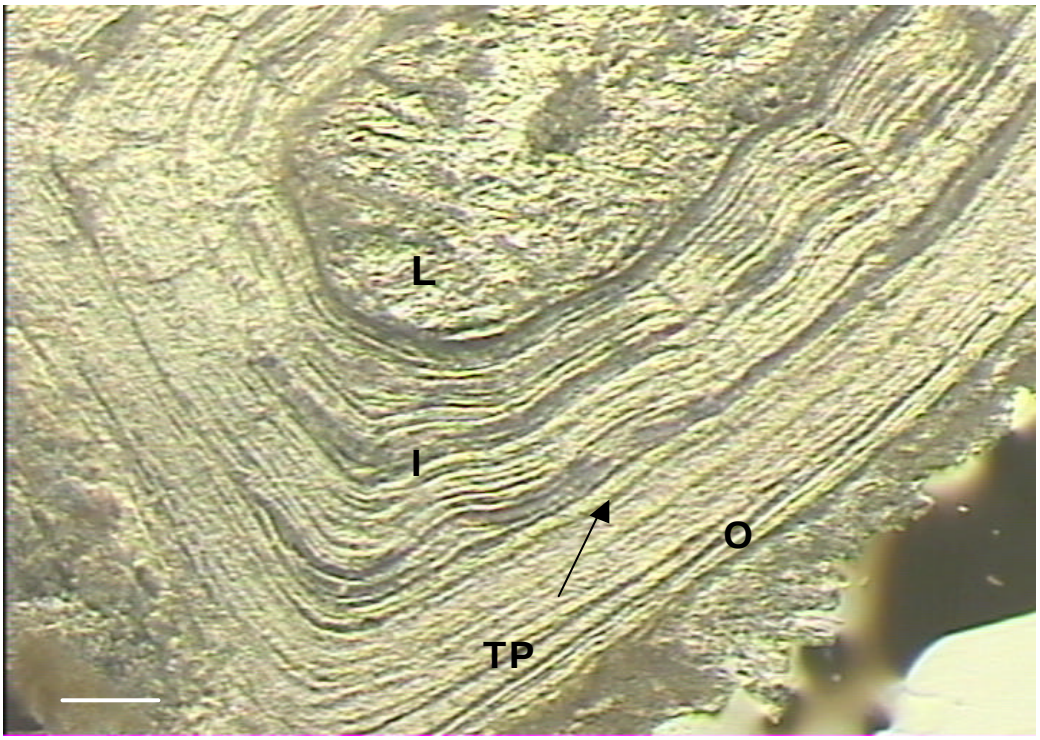

Fig. 3.32. Photomicrograph of cross section of 1st dorsal spine of an 87 cm TL male *Deania calceus*, estimated age 18 years, (x 40) showing bands in the inner (I) and outer (O) trunk layers, separated by trunk primordium (TP). Lumen (L) to centre. Scale bar: 500 µm.

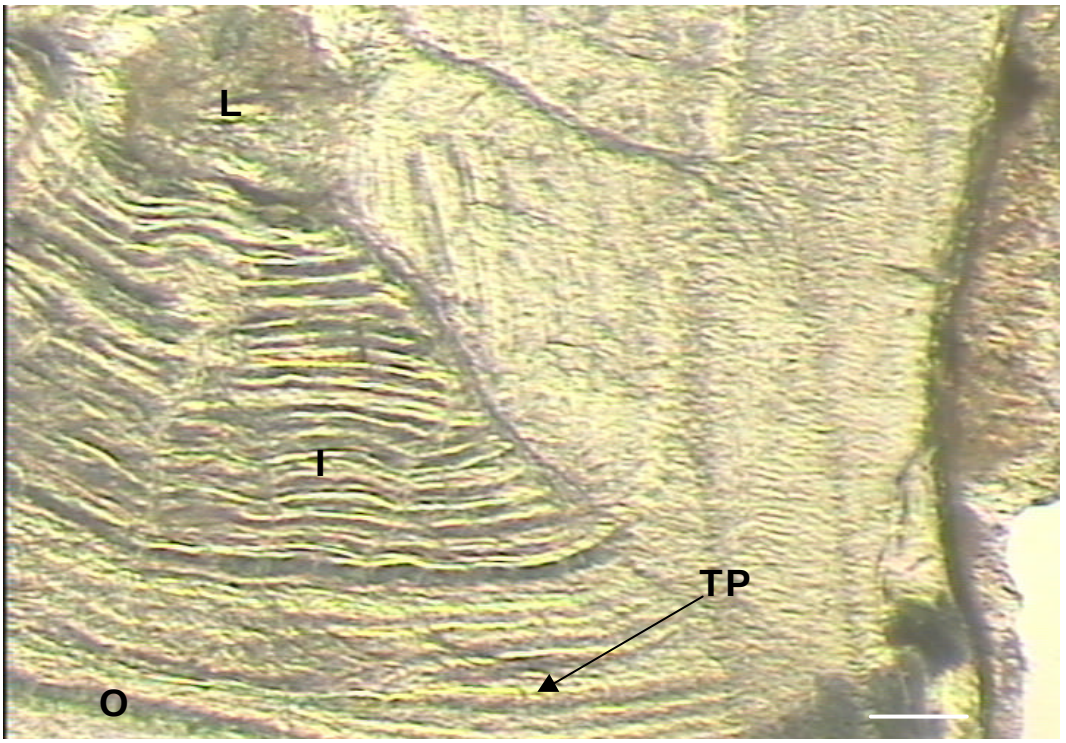

Fig. 3.33. Photomicrograph of cross section of 2nd dorsal spine of a 101 cm TL female *Deania calceus* (x 40) showing bands in the inner (I) and outer (O) trunk layers, separated by trunk primordium (TP). Lumen (L) to centre. Scale bar: 500 µm.

4 Discussion

Adequate scientific information is required for sustainable management of deepwater fish stocks (Hopper, 1995). The present study sought to provide this information for three exploited deepwater squalid shark species. It was carried out as part of an international research programme PL 95 0655 (EC FAIR, 1999) that aimed to collate and analyse existing survey data and investigate the biology of certain species, including an analysis of catch and discards. The present study was based on an extensive deepwater survey programme of the Rockall Trough and Porcupine Slopes carried out by the Marine Institute (Kelly *et al*., 1998) see Appendix VII for details. The dearth of scientific data has prevented the stock assessment of deepwater species. In particular little information on the biology, fisheries or management of deepwater sharks exists in the scientific literature. This study provided new information on the vulnerability of these species to trawls and long-lines. Age estimation techniques were developed for the first time for two of the species, though not for *Centroscymnus coelolepis*. All the species were shown to have low reproductive outputs, and for *Centroscymnus coelolepis* and *Deania calceus*, a period of time elapses after parturition, before a subsequent gestation ensues. In all cases smallest sharks were absent from the study area, even though their entire depth ranges were sampled. No seasonal cycle in reproduction was found for *Centroscymnus coelolepis*. However a lack of samples from throughout the year prevented a full analysis of seasonal cycles in *Deania calceus* and *Centrophorus squamosus*. This study provides basic information on the life history of these exploited species and will facilitate the development of management measures to ensure a sustainable fishery.

4.1 Missing size ranges

An important finding is the absence of smaller specimens of these species from the study area. A possible explanation for this absence is that they are in fact present in the study area but not selected by the trawl or long-line gears employed. However, several findings of this study suggest that this is not so. Small (7/0 EZ) hooks were deployed during the long-line surveys in 1997 and 1999 in an attempt to target small sharks. Yano and Tanaka (1984) and Silva (1988) also, unsuccessfully used smaller hooks to target smaller squalid sharks. Both commercial-size and small hooks used in this study

captured specimens of the squaliform shark *Etmopterus princeps* as small as 27 cm TL (Connolly *et al.*, 1999). This is only a few centimetres longer than near-term embryos found in gravid female *Deania calceus* and smaller than either near-term embryos of *Centroscymnus coelolepis* recorded in the present study, the near-term embryo of *Centrophorus squamosus* recently found at Madeira (Hareide and Stehmann, *pers. comm*.) or free-swimming immature specimens caught off Portugal (Figueiredo *pers. comm*.). Data from the present study suggest that smaller hooks do not select for smaller squaliform sharks and that standard (13/0 EZ) hooks select for the sharks of 27 cm and upwards.

The trawl net, with fine-mesh liner retained specimens of roundnose grenadier *Coryphaenoides rupestris* as small as 3 cm pre-caudal fin length (Clarke *et al.*, 1999). Selectivity experiments conducted during the 1997 trawl survey showed that the 105 mm cod end retained *Coryphaenoides rupestris* as small as 3 cm pre anal fin length, even when the cod-end liner was not attached (Kelly *et al.*, 1998). *C. rupestris* of 3 cm pre-caudal fin length are much smaller than near-term embryos of any of the species under study. Therefore it seems unlikely that small sharks could escape through the meshes of the cod-end. Extensive coverage of the continental slopes west of Scotland and Ireland was achieved in this study. The selectivity of the long-lines for small sharks and of the trawls for small *C. rupestris* suggest that the absence of smaller specimens cannot be explained by the selectivity of the fishing gears used. Another explanation for the absence of these small specimens must be found.

Other studies of deepwater species have noted the absence of smaller squaliforms from particular areas (Girard and Du Buit, 1999; Gordon *et al.*, 1995a; Yano and Tanaka, 1984). While *Centroscymnus coelolepis* as small as 32 cm TL were recorded in trawl surveys off Namibia by Ebert *et al.* (1992) this is the only published account of small specimens of this species. A small specimen (35 cm) of this species in the possession of the Virginia Institute of Marine Science was located in Norfolk Canyon, off NE USA (Musick and Gelsleighter, *pers. comm*.). However other studies of this species were characterised by the lack of small specimens (Girard and Du Buit, 1999; Yano and Tanaka, 1988). The absence of smaller specimens of *Centrophorus squamosus* has been documented by Girard and Du Buit (1999). Again the only published record of small

specimens of this species is that of Ebert *et al*. (1992) which documents specimens as small as 43 cm off Namibia and South Africa. The only records of gravid female *Centrophorus squamosus* are from Madeira (Hareide and Stehmann, *pers. comm*) and continental slopes of Portugal where small free-swimming specimens are present also (Figueiredo *pers. comm*.). Yet small *Centroscymnus coelolepis* were absent from west of Ireland despite the presence of gravid females. This finding suggests that the smaller sharks may have a different bathymetric distribution. Perhaps localised hydrographic conditions determine the presence or absence of small sharks on the continental slopes.

Girard and Du Buit (1999) describing the absence of small size ranges of *Centrophorus squamosus* and *Centroscymnus coelolepis* suggested they might be present on the Mid-Atlantic Ridge. Their presence in that region may indicate a cyclical migration pattern in the northeast Atlantic. Recent work by Hareide and Thompson (1987) showed that the species under study do inhabit the waters of the Mid-Atlantic Ridge but no small specimens were found. The continental slopes of Portugal are also populated by *Deania calceus* of smaller size than those present west of Ireland. Indeed there is little overlap in the lengths of male or female *Deania calceus* from the present study and those taken from surveys off Portugal (Machado and Figueiredo, 2000). However these authors do not state in which depth range these smaller *Deania calceus* were found. Clark and King (1989) found that smallest *Deania calceus* associated with large females in waters to about 800 m, and a progressive increase in their numbers moving west to east around North Island New Zealand. This finding may indicate a cyclical migration with small sharks present in localised areas.

The presence of certain sizes or reproductive phases in areas of the continental slope and their total absence from others, as in the case of *Deania calceus* and *Centrophorus squamosus*, may suggest complicated migration patterns linked with reproductive activity. In addition it seems likely that breeding aggregations are localised, as suggested by Clark and King (1989).

Muñoz-Chapuli (1984) hypothesised that slope-dwelling demersal sharks have nursery grounds on the continental shelf to which pregnant females migrate, while adult males remain at greater depths. Such a strategy would prevent intra-specific competition

according to this author. There was a tendency for gravid female *Centroscymnus coelolepis* to occur in shallower waters. However no evidence for the presence of smaller specimens in shallow water nursery grounds was found. While gravid females occurred in shallow waters they did not occur in shelf waters.

Evidence for this can be found in information collected by Marine Institute observers and from international bottom trawl surveys. For the duration of this study (1996 – 2000) observers were engaged in monitoring discards onboard prawn *Nephrops norvegicus* trawlers on the Porcupine Bank (Clarke 1999a). Results confirmed that the squaliform sharks *Etmopterus spinax* and *Dalatias licha* were present in this area. However no specimens of the species under study were ever obtained (Laide; Ní Chonchúir; Bermingham, *pers. comm.*). The Marine Laboratory, Aberdeen, Scotland, conducted a trawl survey for monk-fish *Lophius* spp. and megrim *Lepidorhombus* spp. in March 2000 on the slopes of the Rockall Trough from 200 m – 1,000 m. No small specimens of any of the sharks under study were recorded (Lordan, 2000). Thus no small specimens of these species occur on the shelf edge or in the deeper parts of the shelf, west of Ireland. However the tendency for gravid females to occur in shallower waters may support the hypothesis of Muñoz-Chapuli (1984) that slope-dwelling demersal sharks move up-slope for parturition and return to deeper waters afterwards. While Munoz-Chapuli's theory may describe the movements of some shark species, the data available on the species under study does not support the view that nursery grounds occur on the shallower grounds.

Another possible explanation for the missing size ranges is that they are present in pelagic waters. Such a distribution would agree with that described for *Squalus acanthias* in which parturition occurs in pelagic waters of 145-155 m over-lying depths of up to 250 m (Ketchen, 1986). This species spends its juvenile life in mid-water where its food consists predominantly of small invertebrates, but the diet changes to fish with increasing size (Jones and Geen, 1977b). It seems likely that the prey preferences of other squalid sharks change with size also. Mauchline and Gordon (1983) found that the larger, demersal, shark species of the Rockall Trough were consumers of fish but that the smaller species, present some distance off the bottom consumed micro-nekton. These prey preferences are probably a function of size. Previous studies have found that smaller sharks have differing prey preferences to larger specimens. The size-dependent

prey preferences of slender smoothhound *Gollum attenuatus* have been described by Yano (1993) and of black dogfish *Centroscyllium fabricii* by Jakobsdottir (1998). It is possible that neonatal and small squaliform sharks have different prey preferences and may live among the mesopelagic fauna, or in one of the deep scattering layers. Such a strategy would also protect these specimens from predation by larger squaliform sharks.

Evidence for a more pelagic distribution of smaller specimens of the species under study may be found by comparison of length frequencies for trawl and long-line. Long-lines took smaller specimens of *Centroscymnus coelolepis* than trawls. This result suggests these smaller sharks occur at some distance from the sea-bed, out of the range of trawls (headline height around 4 m), but attracted to the baited hooks. The presence of mesopelagic organisms in stomachs of *Deania calceus* (Yano, 1991) may suggest a mesopelagic distribution for this species. Its elongated snout suggests an enhanced ampullary system and the posterior position of the dorsal fins and the paddle-like pectorals, a high degree of manoeuvrability in the vertical plane (Tabit, 1993). Bridger (1978) found mackerel *Scomber scombrus* and scad *Trachurus trachurus* in stomachs of this species and suggested that it might make extensive vertical migrations in search of food. The presence of meso- and epi-pelagic fauna in the diets of this species may suggest that it is not exclusively demersal. However it may prey on these fauna as they impinge on the continental slopes, or during their diurnal vertical migrations as described by Mauchline and Gordon (1991).

The possibility of missing size classes of deep demersal fish occurring in more pelagic waters needs further consideration. This hypothesis has been put forward by Haedrich (1997) for the absence of small sharks and black scabbards *Aphanopus carbo* from bottom trawl catches. Mid-water trawls have seldom been used for research purposes (Merrett, 1986) so the vertical distributions of demersal fishes are poorly understood (Merrett and Haedrich, 1997). One of the few studies to document small squalid sharks was that of Clark and King (1989) who actually used mid water trawls. Unfortunately they did not state whether the small size ranges of *Deania calceus* they recorded were pelagic or demersal in their occurrence. To investigate whether small deepwater sharks and other fish species are present in pelagic waters will require the extensive use of mid-water trawls, in addition to demersal trawl nets.

4.2 Distribution and Abundance

Centroscymnus coelolepis was more abundant on the western Porcupine slopes than on the eastern slopes of the Rockall Trough. However catch rates were low in the Porcupine Seabight. Bridger (1978) noted that this species occurred "rather spasmodically" in trawl catches in these areas and Magnusson and Magnusson (1995) noted that the species was common but never very abundant in trawl catches on the Reykjanes Ridge, south of Iceland. Peak CPUE for *Centroscymnus coelolepis* was between 1,300 and 1,400 m, agreeing well with previous studies of this area (Gordon, 1999). Gordon also suggests that because most deepwater fishing takes place in shallower depths this species will escape most fishing pressure. The depth range west of Ireland is similar to that for Japan (600 m and 1,300 m) (Yano and Tanaka, 1988) and off Namibia (660 m – 1,016 m) (Ebert *et al.*, 1992). However in the Catalan Sea, western Mediterranean, *Centroscymnus coelolepis* is only found in much deeper waters from 1,400 to 2,200 m, and very rare in waters less than 1,600 m (Carrasson *et al.*, 1992).

Several authors have described differing frequencies of each sex with depth in squalid sharks. Female *Centroscyllium fabricii* were found to out-number males in the deeper part of their depth range (Jakobsdottir, 1998; Yano, 1995). Jakobsdottir reported a similar trend for *Etmopterus princeps*, agreeing with the present study for *Centrophorus squamosus*. In contrast female *Centroscymnus owstoni* predominated in shallow water gill-net catches (Yano and Tanaka, 1984), agreeing with the results of present study for female *Centroscymnus coelolepis*. The reasons for these differences are unclear. Interestingly Jakobsdottir's (1998) study of *Etmopterus princeps* and *Centroscyllium fabricii* found only small numbers of mature females, similar to the results for *Centrophorus squamosus* in the present study. This may indicate some form of reproduction-related movement of females of those species away from their respective areas of reference.

Pre-ovulatory *Centroscymnus coelolepis* females and stage 3 ripe males were found in greatest numbers in the same depth intervals of 1,000 to 1,100 m, suggesting that mating occurs in these depths. There was also an increase in the numbers of immature specimens with depth. An interesting aspect of this study was the almost complete absence of

gravid females from waters deeper than 1,300 m. Gravid female *Centroscymnus coelolepis* occurred almost exclusively in shallower waters, though post-natal sharks were most numerous in the deeper segments of the range. Girard and Du Buit (1999) also found a predominance of mature males and pre-ovulatory females in the middle of the depth range of this species and reported an increase in numbers of immature specimens with depth. These authors and Yano and Tanaka (1988) also report that gravid females were present in shallower waters. However in Yano and Tanaka's study these females were found in depths of between 100 and 600 m, and were the only specimens encountered at those depths. Segregation of maturity stages in deepwater sharks was described by Tanaka *et al.* (1990) for *Chlamydoselachus anguineus*, Yano and Tanaka (1988) for *Centroscymnus coelolepis* and *C. owstoni* and Hanchet (1988) for *Squalus acanthias*.

Centrophprus squamosus is most abundant in catches on the eastern slopes of the Rockall Trough. Bridger (1978) also reported that this species was most numerous in this area. The depth range of this species means that it is more vulnerable to fishing than *Centroscymnus coelolepis*, the other commercially important deepwater shark for trawlers in the NE Atlantic. While long-lining caught *Centrophorus squamosus* in deeper waters than trawling it is clear that most of the depth range of this species is within the range of the larger deepwater trawlers. Males dominated in shallower waters, females in the deepest parts of this species' range. However, maximum numbers of ripe males and pre-ovulatory females were found in the middle ranges, suggesting, as with *Centroscymnus coelolepis*, that the sharks converge to mate in these intermediate depths. An interesting feature of this study was that the female population of *Centrophorus squamosus* was dominated by immature specimens, while the males were mostly ripe. Girard and Du Buit (1999) also noted this feature of the *Centrophorus squamosus* population west of Ireland and suggested that their sampling was "incomplete". However, the present study made extensive use of long-lines and trawls with small-mesh cod-end and also found very few mature females in this area. The size ranges of *Centrophorus squamosus* from trawl and long-line were not significantly different. On the other hand larger females of *Deania calceus* and *Centroscymnus coelolepis* were taken on long-lines indicating that they escaped the towed gear. It seems reasonable to conclude that larger female *Centrophorus squamosus* were mainly absent.

Marked declines in CPUE over a 20 year period were reported by Graham *et al*. (1997) based on two trawl surveys. CPUE from orange roughy trawl surveys showed a "general decline" in the abundance of fish and shark by-catch in New Zealand since 1984 according to Clark *et al*. (2000). However their data do not fully support that statement. Biomass estimates of *Deania calceus* almost doubled and that of *Centroscymnus crepidater* increased by more than three times. Biomass of Plunket's shark *Centroscymnus plunketi* did decline, but as for the other species there were considerable annual fluctuations in the data. There was some indication of a decline in CPUE of *Centrophorus squamosus* between the 1996 and 1997 trawl surveys, particularly on the Donegal slope (Section 3.3.5). This may not be indicative of a stock decline, however. Pawson and Vince (1999) cautioned that local increases may be the result of an influx of fish to a particular area and that wide fluctuations in abundance of highly migratory sharks may not reflect overall stock trends. Clark *et al*. (2000) noted that their trawl surveys were designed specifically for *Hoplostethus atlanticus* and may not reflect the true abundance of other species. It is not clear if existing trawl survey CPUE is a useful index of stock abundance in squlaid sharks.

Declining CPUE from French trawlers for *Centrophorus squamosus* and *Centroscymnus coelolepis* has been documented by Lorrance and Dupuoy (1998). Their CPUE series was based on combined catches of the two species. Gordon (1999) reflecting on these declines considered these sharks to be more resilient than some of the teleost species that displayed more marked declines. In particular the CPUE of blue ling *Molva dypterygia* and black scabbard *Aphanopus carbo* from French vessels declined markedly (Lorrance and Dupuoy, 1998). The French fleet has fished progressively deeper to 1,500 m targeting several deepwater species (Anon., 2000b). This movement will have resulted in increased catches of *Centroscymnus coelolepis* and less *Centrophorus squamosus*. Indeed reduced catches of certain species including *Centrophorus squamosus* at depths of around 1,000 m may have led to this movement. Important trends in biomass of either species may have been disguised in the pooled French CPUE data.

Bonfil (1994) already highlighted the problem of the lack of species-specific catch information for many elasmobranchs. Dulvy *et al*. (2000) suggest that aggregated CPUE

series for rays may have disguised the decline of the common skate *Dipturus batis*, which disappeared unnoticed from the Irish Sea (Brander, 1981). The lack of separate catch and effort information for *Centrophorus squamosus* and *Centroscymnus coelolepis* is a serious impediment to the management of the fisheries. The countries with fisheries for these species should ensure that separate catch and effort data are collected.

4.3 Size selectivity of fishing gear

Trawls and long-lines are fundamentally different fishing methods. Trawls herd fish into the opening of the net, while fish are attracted to long-lines by the smell of the bait. This results in both size and species selection (Hareide, 1995). Hareide states that larger specimens of certain species avoid trawls but are caught on long-lines. Since the swimming speed of a fish is proportional to its body size, larger fish will reach baited hooks more rapidly than small fish. Furthermore, research on cod *Gadus morhua* shows that larger fish tend to frighten away smaller ones from baited hooks (Bjordal and Lokkeborg, 1996).

Modal female length of *Deania calceus* from long-lines was much greater than from trawls. Size at 50 % maturity in the population for females (105 cm) corresponds to modal length in long-line catches. Therefore most mature female *Deania calceus* escape trawls, but males are vulnerable to both methods of fishing. In contrast large female *Centroscymnus coelolepis* were selected by both methods, though modal male length on long-line was much greater. Size ranges of *Centrophorus squamosus* from trawl and long-line were not significantly different. Thus mature female *Deania calceus* are more vulnerable to long-lines, and mature *Centroscymnus coelolepis* are vulnerable to both gear types.

Long-lines tend to select for larger teleost fish than trawls (Hareide, 1995; Jorgensen, 1995). Hareide notes that one effect of size selectivity is that more mature fish will be caught by long-lines, and with heavy fishing this could be harmful to the spawning stock. However, as a general rule, fishing of the older part of the stock results in less risk of over-exploitation than fishing of the younger year classes (Hareide, 1995). Based on the results of the present study it seems that this statement may not apply to deepwater shark

species because long-lines are not size-selective. Small specimens of both sexes of *Centroscymnus coelolepis* and male *Deania calceus* taken on long-lines were absent from trawl catches. Furthermore, squalid sharks as small as 27 cm TL were taken on long-lines (Section 4.1). Bait size, rather than hook size is considered to be the most important parameter affecting teleost size selectivity, with smaller fish tending to favour smaller prey items (Bjordal and Lokkeborg, 1996). Results from the surveys upon which the present study is based show that standard commercial hooks and baits select for a broad size spectrum of squaliform sharks representing the entire length range of free-swimming specimens of the species under study. While long-lines have been shown to be a size-selective fishing method for teleosts (Hareide, 1995; Jorgensen, 1995) they do not have any selective properties for squaliform sharks. Thus it appears that small sharks are well adapted to prey on relatively large food items and the results of this study support Gordon's (1999) view that long-lines are not a selective gear type for sharks.

Comparative studies in the Davis Strait found that long-lines were up to 30 times more effective at targeting large Greenland halibut *Reinhardtius hippoglosoides* than trawling (Jorgensen, 1995). Jorgensen demonstrated that a higher yield per recruit would be achieved from long-lining than trawling because of the size selectivity of the lines for that species. The results of the present study indicate that long-lines are not size-selective for sharks. The implication of this result is that fisheries for sharks based on long-lines may not achieve a higher yield per recruit than trawls.

This study made use of fishery dependent (port-sampling) data as well as survey (fishery independent) data. This allowed for an analysis of the size selectivity of commercial and research trawls. There were no significant differences in the length frequencies of *Centroscymnus coelolepis* from French deepwater trawls and Irish deepwater bobbin trawls. Gordon (1999) noted that little was known about the catching efficiencies of deepwater fishing gear but suggested that headline height may be an important factor. The results of the comparison of the size-selectivity of French and Irish deepwater trawls for *Centroscymnus coelolepis* may support this statement, since both trawls under investigation had similar headline heights.

It is clear, however, that smaller female and larger and smaller male *Centroscymnus coelolepis* are present some distance above the bottom, out of the path of trawls, but are attracted to baits. Yano and Tanaka (1984) found highest catch rates of *Centroscymnus coelolepis* from hooks 16.5 m from the bottom, indicating that they are active at considerable heights above the seabed. Larger female *Deania calceus* avoid trawls. This may be because they occur at some distance above the sea-bed, or because they are strong swimmers and escape the towed gear. Video footage of deepwater trawls taken by the Marine Laboratory Aberdeen, Scotland (Newton, *pers. comm*.) shows large *Deania calceus* displaying much manoeuvravibility in the opening of the net. Perhaps the enhanced ampullary system indicated by its elongated snout, and morphology which Tabit (1993) suggested was adapted for quick lunging movements may allow this species to escape towed gears.

4.4 Discarding

Limited information on the combined landings of *Centrophorus squamosus* and *Centroscymnus coelolepis* are available (Anon, 2000b). However since *Deania calceus* is discarded by fishing vessels, it is difficult to quantify catch levels of this species. Connolly and Kelly (1996) provided the first estimates of the tonnage of *Deania calceus* discarded in the Rockall Trough. These authors estimated that 1,155 t of this species was discarded in 1995, based on the weight of roundnose grenadier *Coryphaenoides rupestris* landed and calculated that this represented 256,411 individuals. The estimate of discarding from the present study (745 t) for the Rockall Trough and the slopes of the Porcupine Bank was lower than Connolly and Kelly's (1996) estimate for the Rockall Trough. Connolly and Kelly (1996) estimated discard rates for *Deania calceus* using roundnose grenadier *Coryphaenoides rupestris* as the target species. Highest catch rates of *Coryphaenoides rupestris* were recorded further north in the Rockall Trough (Kelly *et al.*, 1997a) than *Deania calceus*. Furthermore, the depth range of *Coryphaenoides rupestris* 900 m –1,400 m (Blasdale and Newton, 1998) is slightly deeper than that of *Deania calceus*. Blasdale and Newton (1998) stated that the varying depths fished by the boats hamper discard studies in deep waters. French vessels are known to fish over differing depths to target particular species (Charuau *et al.*, 1995). Since trawlers move over different depths to target different species, combining the landings data for the 2

commercial sharks, with different depth ranges allows for a more complete estimate of discarding.

The present estimates were based on the combined landings figures for *Centrophorus squamosus* and *Centroscymnus coelolepis* in ICES sub areas VI and VII. Estimates of discarding based on French landings of "siki and faux siki" show that a considerable tonnage (733 t) of *Deania calceus* was discarded. In contrast estimates of discards from Scottish vessels were only 12 t in 1996. These boats mainly concentrate on the shelf edge, targeting *Lophius* (Gordon, 1999). Since Scottish vessels are not active in the areas south of the $56^{0}30$ N it can be concluded that these vessels do not impact on the populations of *Deania calceus* to any great extent.

Spanish-owned vessels prosecute a fishery for deepwater sharks, including *Deania calceus* on the Porcupine Slopes (Iglesias and Paz, 1995) and the Rockall Trough (Pineiro *et al*., 1998). While they target *Deania calceus*, only the liver is retained (Mulligan, 2000) and the carcass discarded. It is difficult to quantify the catch of this species in this fishery. While these vessels use a different long-line system with the main line off the bottom and the snoods hanging vertically with 10 hooks per snood (Pineiro *et al*., 1998) it is clear that long-lining in this area leads to large discards of *Deania calceus*. It is not possible to estimate the quantities of *Deania calceus* discarded based on the landings of the other sharks because only fillets of these species are landed. However the present study shows that it accounts for a large proportion of catches from long lining on the Porcupine slopes. It can account for as much as 62 % of the total catch in long-lining, depending on the depth fished.

Deania calceus is also discarded in large quantities in the New Zealand orange roughy *Hoplostethus atlanticus* fishery (Bonfil, 1994). From the present study it is clear that trawling produces large discards of *Deania calceus* in the northeast Atlantic. Previous studies of discarding from deepwater trawlers west and north of Ireland concluded that *Deania calceus* was the most dominant species (Blasdale and Newton, 1998; Connolly and Kelly, 1996; Dupuoy *et al*., 1998). While the discard rates of teleosts were different for French high headline trawls and Scottish "scraper" trawls, the discard rate of *Deania calceus* did not differ greatly (Blasdale and Newton, 1998). In view of the depth

distribution of this species, within the scope of deepwater trawlers and long-liners, and its wide geographical range it seems likely that it is subject to heavy pressure from different gear-types in several parts of the world. Therefore estimates of the level of discarding in other areas where this species is a by-catch are urgently required. The deep waters of Namibia may require attention in this regard since this species occurs (Ebert *et al*., 1992; Yano, 1991) and fishing has recently commenced (Merrett and Haedrich, 1997).

It is considered unlikely that discarded deepwater species, including sharks could survive (Connolly and Kelly, 1996; Gordon *et al*., 1995a). Research in Australia showed that most discards from trawlers were dead, about 50 % floated and were scavenged by seabirds, dolphins and sharks, the remainder was consumed by sharks in mid-water and by sharks, teleosts and crustaceans on the bottom (Hill and Wassenberg, 1990; Wassenberg and Hill, 1989). Thus scavenging species, especially sharks, may benefit from discards as food. The increased abundance of the starry ray *Raja radiata* in the North Sea may be due to its scavenging habits according to Walker (1999) while Harris and Poiner (1991) suggested that discards from commercial fisheries might be a factor in the increased abundance of charcharhinid sharks off south Australia. In view of its scavenging habits (Clarke and Merrett, 1972) *Centroscymnus coelolepis,* of the species under study may be most likely to benefit from discards.

While the environmental impacts of discarding in shelf waters have received some attention (Jones, 1992; Lindeboom and de Groot, 1998) little work on this topic exists for deep water. Clucas (1997) suggested that oxygen depletion of water bodies caused by the decomposition of discards on the sea bottom may impact on the benthic community, but notes that the effects of destruction of habitat caused by the gear itself (particularly bottom trawling) and inputs of carrion are difficult to separate. Recent surveys of the seabed west of Scotland have shown widespread damage to the sea floor and benthic in-fauna by deepwater trawlers (AFEN, 2000). The paucity of information on the effects of trawling on the deep sea bed has already been noted by Jones (1992). Future evaluations of discarding of deepwater species, such as *Deania calceus,* should aim at an understanding of the impacts of inputs of large amounts of carrion to the deepwater

ecosystem. However such studies may be difficult to undertake in deep waters (Kelly *et al.*, 1998).

4.5 Variation in GSI and HSI

While each parameter has been dealt with, little information on the relationship between GSI and HSI exists in the scientific literature. Yano (1995) reported a decrease in HSI during maturation and pregnancy in female *Centroscyllium fabricii* only recovering in post-natal females. This finding accords with the present study of *Centroscymnus coelolepis*, where HSI declined during maturation and pregnancy. In contrast HSI actually increased in pre-ovulatory *Centrophorus squamosus*. In *Scyliorhinus canicula* Craik (1978a) found that the variation in HSI was greater for females than males. This agrees with the findings from the present study, where HSI for females varied more widely among maturity stages. Rossouw (1987) pointed out that Craik's data also showed that the female liver is only larger than that of the male at certain periods of the annual cycle of *Scyliorhinus canicula*. While there is no evidence for a seasonal reproductive cycle in the species in the present study (Section 4.6) it is apparent that the size of the liver varies depending on reproductive stage, as described by Yano (1995) for *Centroscyllium fabricii*.

The role of the shark liver in buoyancy control has been the subject of several works (Baldridge, 1972; Bone and Roberts, 1969; Corner *et al.*, 1969; Craik, 1978b). The livers of the 3 species under study all contain large amounts of squalene (Corner *et al.*, 1969). There is evidence that this low-density hydrocarbon is used to provide hydrostatic lift and achieve neutral or near-neutral buoyancy (Bone and Roberts, 1969; Corner *et al.*, 1969). While squalene is a very effective generator of lift per unit of volume, Corner *et al.* (1969) considered it unlikely that this hydrocarbon, once deposited, could be resorbed from the liver. These authors felt that the fine regulation of buoyancy was probably achieved by lipid regulation. Bone and Roberts (1969) predicted that deepwater sharks must maintain a fairly constant percentage weight in ambient water by regulating the density of their livers or other tissues. Corner *et al.* (1969) also observed that ripe oocytes of *Centroscymnus coelolepis* approached neutral buoyancy at the surface, but

with the liver removed the specimen examined became 4 % denser than surface seawater. Thus the ovaries of ripe females generate lift also.

Craik (1978a) found that variations in HSI in *Scyliorhinus canicula* were linked to vitellogenesis and argued that the primary reason must be deposition of lipid at times of food abundance and utilisation of these reserves when food is scarce. The demands of vitellogenesis in *Centroscymnus coelolepis*, which produce very large oocytes, probably account for the decrease in HSI during maturation. Since the oocytes themselves generate considerable lift (Corner *et al*., 1969) a reduction in the size of the liver may serve to maintain neutral buoyancy. The demands on lipid reserves during pregnancy may also lead to a reduction in size of the liver. Tanaka *et al*. (1990) suggested that feeding in pregnant sharks is impaired because of lack of space in the body cavity and consequently lipids would not be available for deposition in the liver. Bone and Roberts (1969) investigated the lift generated by the livers of gravid specimens of *Squalus acanthias* and suggested that the density of the fish is regulated during pregnancy. The differing demands of vitellogenesis in *Centrophorus squamosus* and *Centroscymnus coelolepis* may explain the different relationships between GSI and HSI in these species. The ovaries of stage 3 *Centroscymnus coelolepis* account for twice the percentage body weight compared to *Centrophorus squamosus*. Thus the demands of vitellogenesis on the liver of *Centrophorus squamosus* are likely to be lower than on *Centroscymnus coelolepis*. This may explain why HSI does not decrease during vitellogenesis in *Centrophorus squamosus*.

It is beyond the scope of this study to investigate whether sharks maintain a fine balance between the buoyancy of their livers and gonads in order to regulate hydrostatic lift. However based on the variations in GSI and HSI in *Centroscymnus coelolepis* and the similar pattern reported by Yano (1995) for *Centroscyllium fabricii* it seems that this is likely. Of six shark species examined by Craik (1978b) only the liver of *Squalus acanthias* contained low density lipids. Craik speculated that since this species lives in deeper waters than the other species it required these low density lipids to generate lift. This author also suggested that if species such as this did not have this mechanism they would not be able to escape the bottom, and in the case of deepwater species this would be a distinct disadvantage. Wetherbee (1998) considered that there is a strong selection

pressure for neutral buoyancy among deep-sea sharks due to the energetic constraints of the deepwater environment.

An important aspect of the reproductive cycle of many deepwater sharks is that they do not carry ripe or ripening oocytes during gestation. In the present study GSI in *Centroscymnus coelolepis* was low during gestation, only increasing in post-natal females. Ovarian development does not occur during pregnancy in *Deania calceus,* though it does in the case of *Centrophorus squamosus* (Yano *pers. comm*). This has already been described for *Centroscymnus coelolepis* (Girard and Du Buit, 1999; Yano and Tanaka, 1988), *Centroscyllium fabricii* (Yano, 1995) and the frilled shark *Chlamydoselachus anguineus* (Tanaka *et al*., 1990). Tanaka *et al*. (1990) considered that oocytes do not develop during gestation because of a lack of space in the body cavity. However this is not the case for all squalid sharks; *Squalus acanthias* (Holden and Meadows, 1964) and *Centrophorus granulosus* (Capape, 1985) are examples of species that do have concurrent ovarian and uterine development. Holden (1974) and Gauld (1979) described density dependent changes in fecundity of *Squalus acanthias* due to increased exploitation. Non-concurrent ovarian and uterine cycles implies that these deepwater species have a lower reproductive potential than *Squalus acanthias*, which may suggest that such responses to increased exploitation will be slower.

4.6 Reproduction

Pratt and Otake (1990) recommended that in assessing maturity of elasmobranchs the presence of ripe sex products, such as sperm or ripe oocytes, should be considered. The maturity scale used in the present study (Appendix III) fulfilled these requirements for both sexes. The scale proved difficult to use for female *Centrophorus squamosus*, where no uterine stage females were ever recorded, though some females were identified as post-natal, based on flaccid ovaries, with degenerate follicles and distended uteri. Analysis of uterine width data supported the designation of these females as post-natal. Girard and Du Buit (1999) assigned a small number of female *Centrophorus squamosus* to the post-natal maturity stage 7. They cited the increased villification of the uteri of these fish as a criterion in their decision. Yano and Tanaka (1987) also noted an increased vilification in the uteri of post-natal *Centroscymnus. owstoni* and *Centroscymnus coelolepis*. These villi are typical of viviparous yolk-sac dependent

species according to Otake (1990). The percentage of stage 7 females in Girard and Du Buit's (1999) study was less than 1 %, somewhat less than the percentage in the present study (4 %). This is probably due to the presence of larger numbers of long-line caught specimens in the present study.

In those species with defined seasonal reproductive cycles certain maturity stages predominate at certain times of the year. *Squalus acanthias* off New Zealand displayed a cycle whereby maximum number of post-ovulatory females with candled ovaries occurred in September and October with late term embryos most numerous from January to May (Hanchet, 1988). Hanchet presents a striking seasonal cycle in the appearance of maturity stages. No such cycle was displayed by any of the species in the present study, nor was such a cycle demonstrated for other deepwater squaliform sharks; *Centroscymnus owstoni* (Yano and Tanaka, 1988) or *Centroscyllium fabricii* (Yano, 1995). Several authors have described marked seasonal cycles in elasmobranch testes (Dobson, 1974, in Hamlett, 1999; Maruska, 1996; Parsons and Grier, 1992; Simpson and Wardle, 1967 and Teshima, 1981. However no evidence was found for such a cycle in the species under study.

The lack of a seasonal cycle in male reproduction was described for *Centroscymnus coelolepis* and *Centrophorus squamosus* by Girard and Du Buit (1999). Yano and Tanaka (1998) found no evidence for a seasonal cycle of spermatogenesis in *Centroscymnus coelolepis* or *C. owstoni*. Using monthly GSI data Yano (1995) found no evidence of seasonal cycle in *Centroscyllium fabricii* testes. In a study of possible environmental controls of male reproduction in *Scyliorhinus canicula* Dobson and Dodd (1977) concluded that temperature was shown to be the main trigger in the seasonal testicular cycle, and not photoperiod as in the case of several teleosts (De Vlaming, 1972). Since temperature is relatively constant in the deep waters (Merrett and Haedrich, 1997) there is probably no environmental signal that could influence spermatogenesis. In a discussion of seasonal testicular cycles of elasmobranchs Parsons and Grier (1992) suggested that in areas where there is little variation in environmental parameters, such as the tropics and the deep-sea, seasonal cycles of spermatogenesis are unlikely. The absence of a seasonal reproductive cycle in males or females of any of the species has important implications for fishery management. Current management policies tend to set

catch quotas on a yearly basis. Merrett and Haedrich (1997) suggest that to maintain a large number of reproductive-aged individuals, management should be conducted at a temporal scale equal to that of the reproductive cycles of the fish populations. However, this seems a difficult goal to achieve.

As noted by Yano and Tanaka (1988) it is difficult to estimate the length of gestation of a species when it does not exhibit clear seasonal periodicity in reproduction. Gestation period in any of the species under study remains unclear but it may be as long or longer than 2 years as in the related species *Squalus acanthias* (Hanchet, 1988) or as long the 39 month-gestation estimated for the deepwater *Chlamydoselachus anguineus* by Tanaka *et al.* (1990). Measurement of *corpora lutea* may provide a means by which to determine the duration of gestation according to Hisaw and Albert (1947) since these bodies display a progressive decrease in size after ovulation. In the absence of a clear temporal cyclicity in the occurrence of maturity stages, this approach may provide the only option available to determine the duration of the gestation period in deepwater squalids.

Analysis of uterine data of *Centrophorus squamosus* suggests a protracted period of rest during which the uteri recrudesce. Clark and King (1989) found only 25 % of female *Deania calceus* in New Zealand in any stage of reproductive development and suggested a resting period of 4 years between reproductive episodes. The very small number of gravid *Deania calceus* (Fig. 4.1) and the complete absence of gravid *Centrophorus squamosus* (Fig. 4.2) from the present study suggest that these females are present elsewhere, therefore it is not possible to draw conclusions about the resting period in these species. However, all female reproductive stages of *Centroscymnus coelolepis* were present only 34 % were in an active reproductive state (Fig. 4.3), suggesting a protracted resting period of around 3 years in this species.

Clark and King (1989) used an 8-point scale for assessing the maturity of *Deania calceus*, including a stage for post-natal females undergoing a subsequent reproductive cycle. Unfortunately these authors do not describe how they defined this stage. However their consideration of resting-ripening females seems valid for iteroparous species since post-natal females must begin the process of vitellogenesis at some point after parturition. The relationship between uterine width and largest ovarian follicle

diameter allows for the elucidation of the reproductive cycle. This cycle in *Centroscymnus coelolepis* is very similar to that displayed by *C. owstoni* (Yano and Tanaka, 1998) and *C. fabricii* (Yano, 1995). In the present study female maturity stage 2, where oocytes are developing, encompasses "virgin-ripening" and "resting-ripening" females. In order to ascertain which of these specimens had in fact carried embryos, and were "resting-ripening" it will be necessary to carry out a histological study of the ovaries. Lance and Callard (1969) conducted a histo-chemical study of the ovary of *Squalus acanthias* and described pre-ovulatory and post-ovulatory degenerate follicles which they termed atretic follicles and *corpora lutea* respectively. These authors were able to differentiate between the two types of degenerate follicles based on the structural analysis of the theca and granulosa. This approach may prove fruitful in determining whether a shark had already carried pups.

Gravid female *Centrophorus squamosus* have been recorded in Madeira (Hareide and Stehmann, *pers. comm.*) and Portugal (Figueiredo, *pers. comm.*). However the present study did not record any gravid females from west of Ireland or Scotland despite intensive sampling. This finding agrees with the that of Girard and Du Buit (1999). In the study area less than 13 % of female *Centrophorus squamosus* were mature. Fig. 4.2 shows the percentage occurrence of each stage of the female reproductive cycle and illustrates the absence of gravid *Centrophorus squamosus* from the study area. The presence of gravid specimens off Portugal and Madeira may indicate a migration linked to the reproductive cycle. It may suggest a possible cyclical migration encompassing the Mid-Atlantic Ridge and the continental slopes of Europe. Very small numbers of gravid *Deania calceus* were recorded in the present study, but their percentage occurrence and the fact that smaller specimens have been recorded off Portugal (Machado and Figueiredo, 2000) suggest that this is a migratory species.

The possibility that migration explains the absence of smaller specimens has already been discussed in Section 4.1. Another deepwater species that is characterised by the absence of small specimens is the black scabbardfish *Aphanopus carbo* (Kelly *et al.*, 1998). Zilanov and Shepel (1975) proposed that this species undergoes a seasonal migration along the continental slope, moving north from Madeira to spawn west of Scotland and Ireland. However this work conflicts with Scottish and Irish studies that

found only immature specimens west of these countries (Kelly *et al*., 1998; Gordon and Swan, 1993). Available evidence does suggest north-south migrations of *Centrophorus squamosus* and *Deania calceus*. The likelihood that many deepwater species are highly migratory underlines the necessity for co-operative international research and future investigations of these species should encompass as wide a geographic range as possible.

A clear finding of this study was that 100 % maturity was not achieved by any length group of male *Centroscymnus coelolepis*. Trippel and Harvey (1989) suggested that this was a feature of populations of slow growing individuals for which sufficient energy was not always available to permit gonadal maturation. Comparison of the present study with the distribution of males of this species by Girard and Du Buit (1999) showed that while they did observe full maturity, many length increments greater than first length at 100 % maturity were accompanied by reductions in the proportions mature. It is surprising, therefore, that the present study did not find 100 % maturity while the study of Girard and Du Buit (1999) in the same area, did. This may be a result of the greater proportions of larger males attracted to baited long-lines, some of which had not attained full maturity. Thus while age estimation was not successful in this species, the distribution of mature males suggests that it is a slow growing species, which may only attain sexual maturity when sufficient trophic resources are available.

Estimates of TL_{50} of *Centroscymnus coelolepis* from the present study and that of Girard and Du Buit (1999) agreed within 1 cm. The only other published details for this species are those of Yano and Tanaka (1988) who reported substantially lower lengths at 50 % maturity from Suruga Bay, Japan. While these authors do not present maturity ogives it is clear that *Centroscymnus coelolepis* in Suruga Bay attained maturity at smaller size than in the area west of Ireland and Britain. In Japan 50 % of males and females were reported to be mature at 70 cm and 95 cm – 99 cm respectively while in the present study the corresponding lengths were 86 cm and 102 cm. However maximum length in Suruga Bay, respectively 92 cm and 108 cm for males and females (Yano and Tanaka, 1984), was also less than observed in the present study, though in both cases 50 % maturity was obtained at similar percentages of maximum length. Furthermore maximum fecundity in Suruga Bay *Centroscymnus coelolepis* was higher than for either study in the Northeast Atlantic.

Girard and Du Buit (1999) speculated that the differences in maximum length, maturity and fecundity in *Centroscymnus coelolepis* may be the result of differing environmental factors in the two areas. This is certainly possible. An alternative explanation is that they may be due to the effects of fishing. A reduction in size at maturity is a well-documented response to exploitation in fish populations (Clark *et al.*, 2000). Yano and Tanaka (1984) stated that squaliform sharks including *Centroscymnus coelolepis* have been exploited in Suruga Bay since the 1940s. It is possible that the differences are due to the effects of sustained fishing over many years. Decreases in size and biomass of several heavily exploited species including Greenland halibut *Reinhardtius hippoglossoides* and golden redfish *Sebastes marinus,* have been recorded in the northwest Atlantic (Haedrich and Barnes, 1997). Changes in fecundity in exploited shark populations were described by Holden (1974), who compared the fecundity of *Squalus acanthias* in the NE and NW Atlantic and suggested the higher values in the NE could reflect decreased abundance of the species due to fishing. Later Gauld (1979) reported increases of 42 % in fecundity in the NE Atlantic. Thus density dependent responses to exploitation may result in increases in fecundity. It is dangerous to speculate on differing biological characteristics of widely separated stocks, yet this point demonstrates the paucity of scientific information on the impact of fishing on deepwater shark populations.

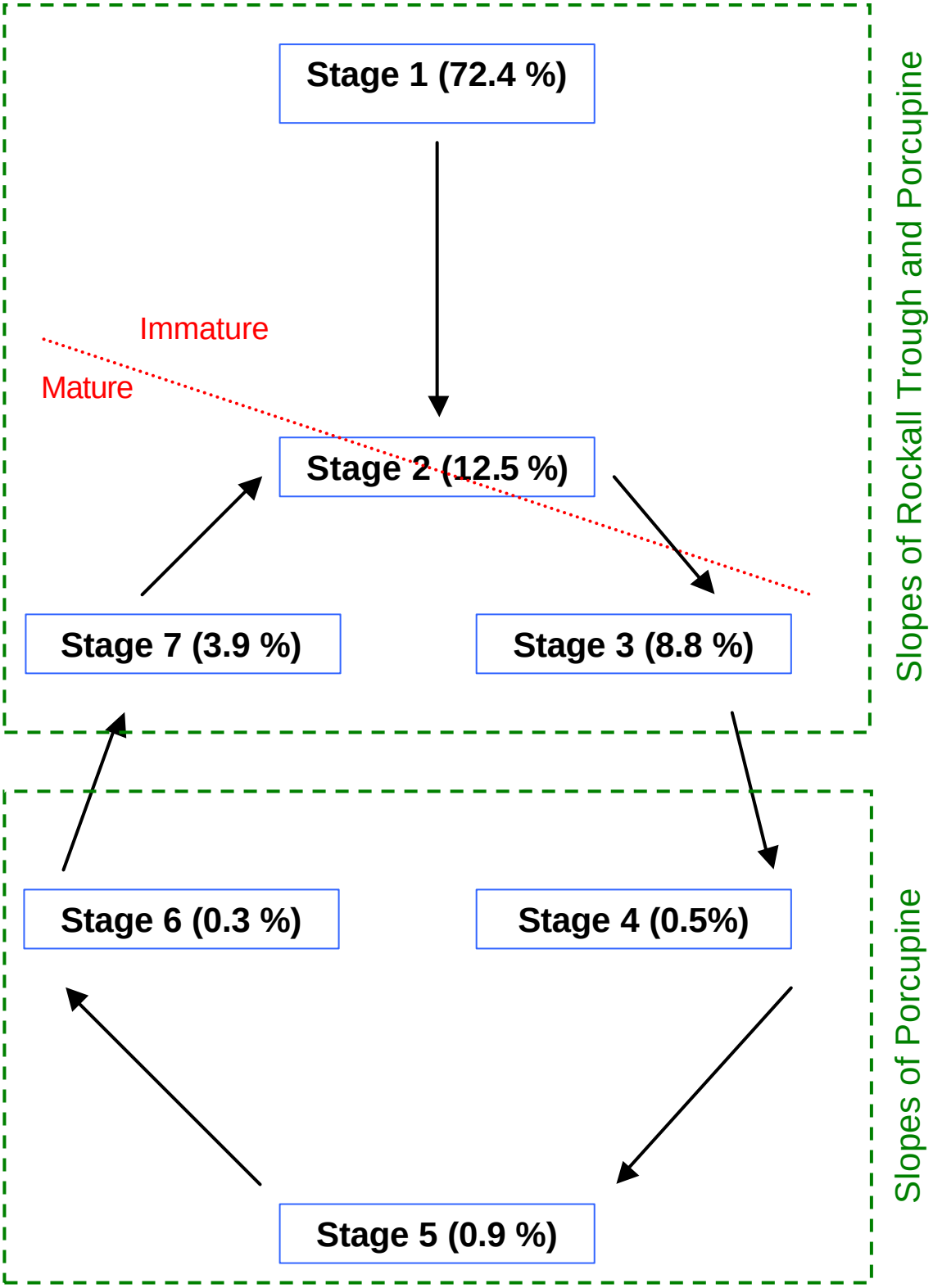

Fig. 4.1. Schematic representation of the reproductive cycle of *Deania calceus* showing percentages of each stage in the study area and the occurrence of gravid specimens. Stage 2 contains both "virgin" and "resting-ripening" females, hence the division between immature and mature.

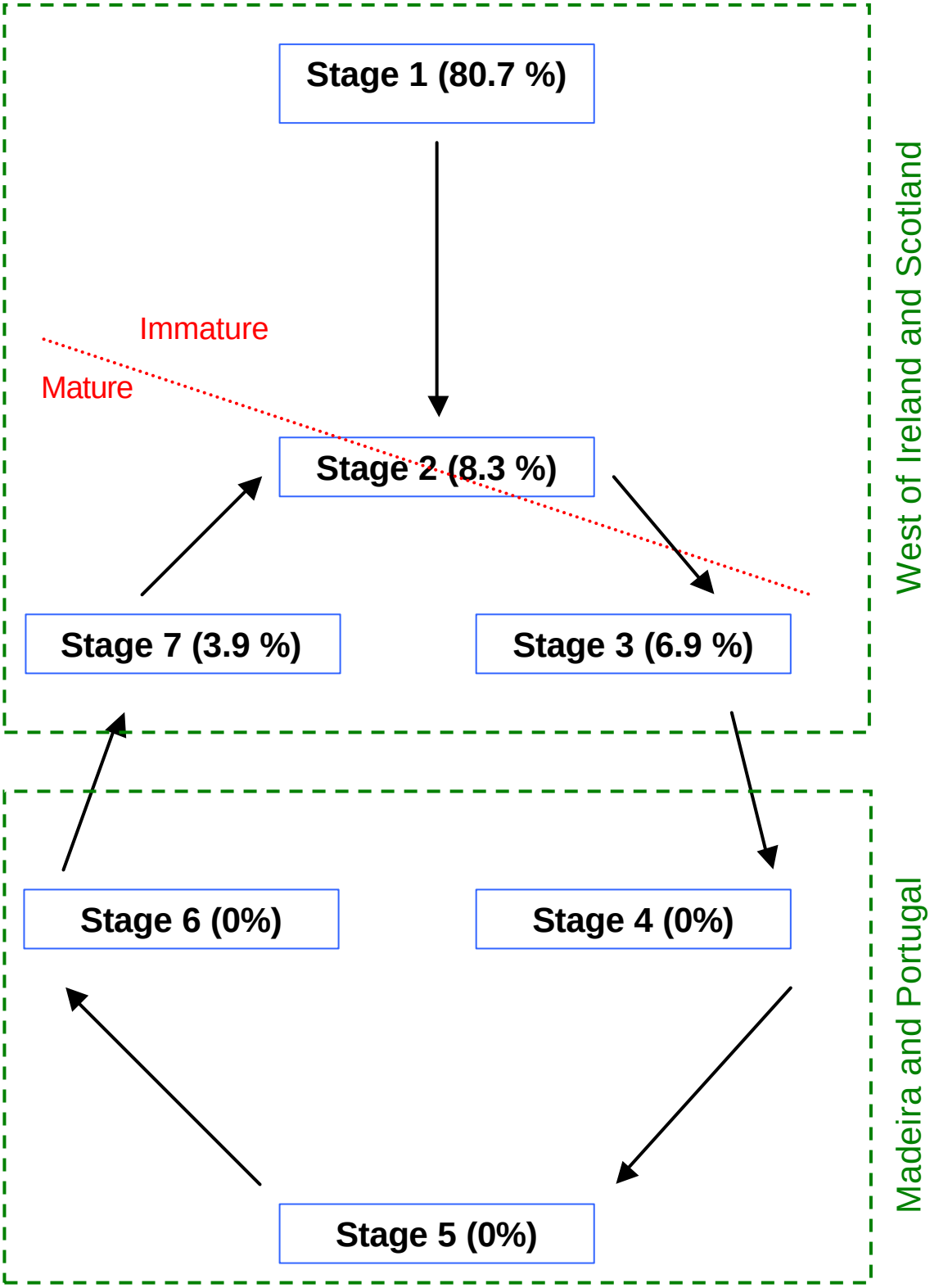

Fig. 4.2. Schematic representation of the reproductive cycle of *Centrophorus squamosus* showing percentages of each stage in the study area and the occurrence of gravid specimens. Stage 2 contains both "virgin" and "resting-ripening" females, hence the division between immature and mature.

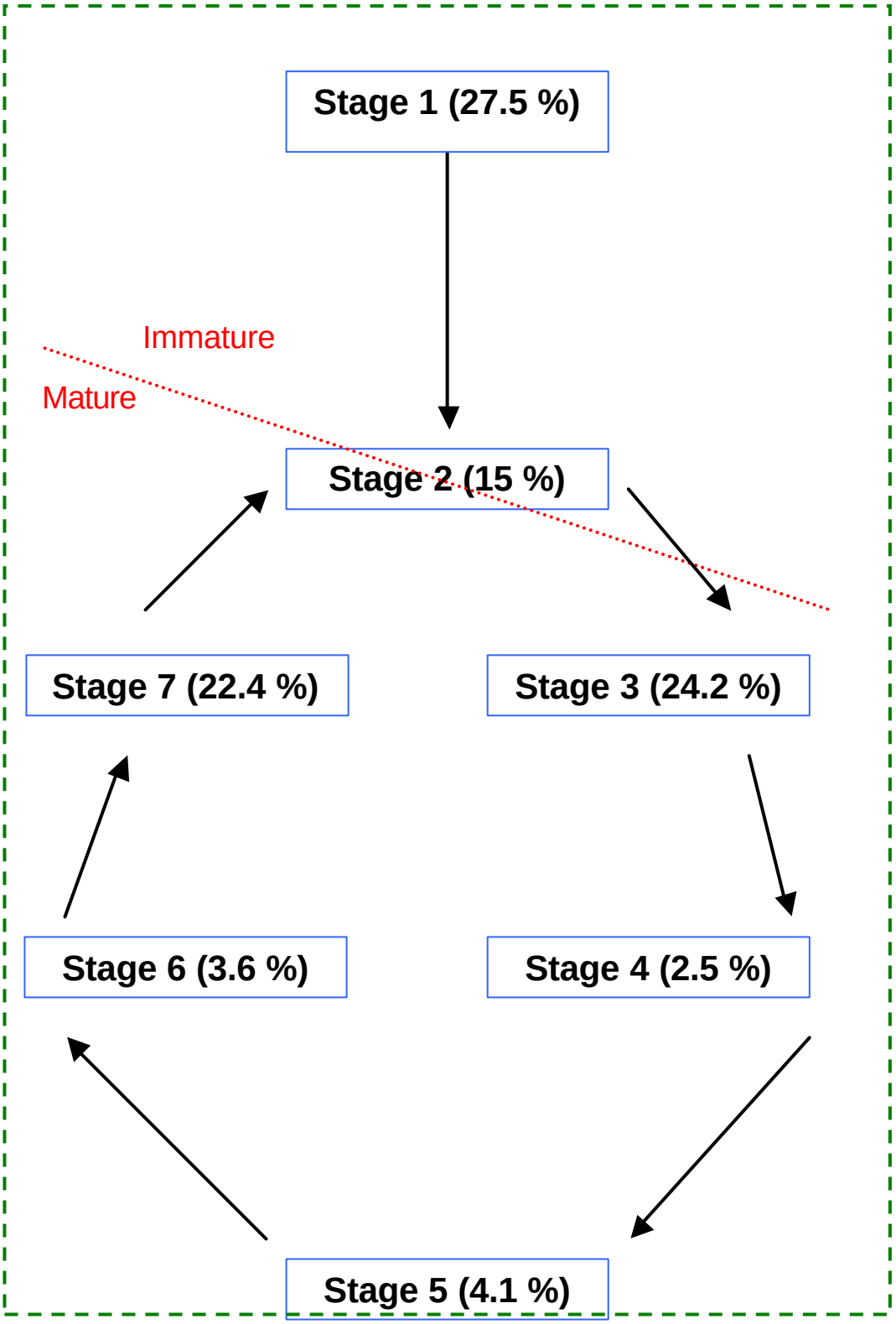

Fig. 4.3. Schematic representation of the reproductive cycle of *Centroscymnus coelolepis* showing percentages of each stage in the study area and the occurrence of gravid specimens. Stage 2 contains both "virgin" and "resting-ripening" females, hence the division between immature and mature.

4.7 Age Estimation

The external and internal morphologies of squalid fin spines have been described in detail by Maisey (1979). The spines of the species under study displayed the same morphology as those described by Maisey and by Guallart Furio (1998) for *Centrophorus granulosus*. While the cap tissues cover the anterior-lateral faces of the spines of *Squalus acanthias*, they are reduced to one or more ribs in the species in the present study and in other deepwater squalids *Centrophorus granulosus* (Guallart Furio, 1998) and *Etmopterus spinax* (Maisey, 1979). In addition to this study other authors who used internal bands for age estimation of squalid sharks were Holden and Meadows (1962) and Soldat (1982) for *Squalus acanthias*, Tanaka (1990b) for *Centrophorus acus*, Guallart Furio (1998) for *Centrophorus granulosus* and Machado and Figueiredo (2000) for *Deania calceus*. Of these studies Holden and Meadows and Tanaka ignored the "middle dentine" layer and probably underestimated age as a result. Guallart Furio, counted bands in the inner trunk layer as in the present study. In the only previous work on one of the species under study, bands were counted in the inner trunk layer, but they appear to have included at least one band from the outer trunk layer in their study (Machado and Figueiredo, 2000, Fig. 2d).

Despite their wide usage in elasmobranch age determination studies (Cailliet, 1990) vertebral centra did not display any banding pattern, despite the use of several staining and sectioning techniques in the present study. Previous attempts to use centra for age estimation of squaliform sharks were unsuccessful (Cailliet *et al.*, 1983; Polat and Gumus, 1995; Soldat, 1982) or inconclusive (Jones and Geen, 1977a). Cailliet *et al.* (1986) suggested that verification of age could be carried out by comparison between methods. Thus, where two or more structures are present the counts from each may be compared. While vertebral centra did not yield band counts in the present study, comparison was possible between 1st and 2nd dorsal spines. Traditionally the percentage agreement of estimates within a certain number of years was used for age verification (Beamish and Fournier, 1981). These authors noted that this method of comparison would not adequately reflect the level of precision citing as examples Pacific cod *Gadus microcephalus* (Kennedy, 1970) and *Squalus acanthias* (Wood *et al.*, 1979). A 95 % agreement within ± 1 year could be very poor precision for *Gadus microcephalus* since

there are only a few year classes in samples. whereas a 95 % agreement of ± 5 years for *Squalus acanthias* could represent very good precision because of the great longevity of this species (Beamish and Fournier, 1981). In this study the average coefficient of variation, expressing the standard deviation as a percentage of the mean was employed and results indicated a good level of precision. Campana *et al.* (1995) recommended this method because it makes use of the standard deviation, and not the absolute deviation as in the case of the average percent error method of Beamish and Fournier (1981).

An important finding of the present study was that there was no significant difference in growth of first and second dorsal spines. In addition a good degree of precision among age estimates from first and second spines was recorded. These findings allowed for the verification of the age estimation technique. However validation of age was not achieved in the present study. Verification is considered to be analogous to determining the precision of an age estimation procedure (Wilson *et al.*, 1983). Cailliet *et al.* (1986) sought to redefine the term verification as "a process of evaluating an assumption, which can only be validated when that process is complete." The present study represents an advance in age estimation methodology for *Deania calceus* and *Centrophorus squamosus*. Further work is required before the process described by Cailliet *et al.* (1986) is complete. In order to complete this task validation of age will be required.

Age estimates of fish must be validated, and validation involves proving that an age estimation technique is accurate, that the bands are annual (Beamish and McFarlane, 1983). These authors considered that validation was complete, only when all reported ages were validated. In their review of ageing studies were separated into two categories. The first contained those studies in which all ages were validated, either by injection with a marker dye and recapture or capture of fish of known age. The second comprised those studies in which only the initial faster phase of growth was validated, by length frequency analysis, monitoring of strong year classes, edge analysis, comparison of different techniques, comparison with back calculated lengths of a corresponding age group. In the areas where smaller and younger specimens of these species are present then validation of the initial growth phases may be possible by one of the techniques outlined by Beamish and McFarlane (1983). Length ranges of *Deania calceus* not present west of Ireland are present off North Island New Zealand (Clark and King, 1989)

and off Portugal (Machado and Figueiredo, 2000). Missing size ranges of *Centrophorus squamosus* are present off Namibia and South Africa (Ebert *et al.*, 1992). In the present study Both *Deania calceus* and *Centrophorus squamosus* are estimated to be very long lived, and the specimens present off Ireland represent larger and older phases of their life histories. In order to validate all reported ages in these species, as required by Beamish and McFarlane (1983), injection of a tissue marking dye is required. Validation by tissue marking dyes has been carried out on vertebral centra by a number of authors; see Cailliet (1990) for a review. However for dorsal spines the only fully successful validation study is that of McFarlane and Beamish (1987b) who injected *Squalus acanthias* specimens with tetracycline, a dye that deposits in calcified tissue.

Validation of age by means of tetracycline (McFarlane and Beamish, 1987a) or one of several other dyes (Walker *et al.*, 1995) is likely to be very difficult to achieve in species that occur in depths of more than 500 m. The only deepwater species for which age has been validated by means of tetracycline injection is the sablefish *Anoplopoma fimbria*, a teleost, which spawns in shallow waters and migrates deeper with age (Merrett and Haedrich, 1997). In this case young specimens were captured and marked in shallower waters. Specimens were at large for up to 11 years and counts of annuli deposited subsequent to injection confirmed that the species attains ages of 70 years (McFarlane and Beamish, 1995). However Yano and Tanaka (1986) successfully attached transmitter-tags to specimens of *Centrophorus acus*, which then returned to their normal depth ranges. Therefore tagging experiments of this and other species of deepwater sharks may be possible in the future.

4.8 Growth and Mortality

The dangers of not validating age estimates, leading to underestimation were highlighted by Beamish and McFarlane (1983) who cited the example of Pacific ocean perch *Sebastes alutus*. Validation of age showed it to be longer lived than previously thought. Based on unvalidated ages, calculated mortality estimates of this species were too high, leading to errors in estimates of stock production (Beamish and McFarlane, 1983). Traditional yield analyses in fisheries science predict that fish stocks with high growth rates and large values of the von Bertalanffy parameter K will require a higher fishing mortality (greater effort) to give maximum yield (King, 1995). The errors in ageing of *Sebastes alutus* led to a management strategy, which in the light of age validation could have been more conservative (Beamish and McFarlane, 1983).

For comparative purposes von Bertalanffy parameters of *Squalus acanthias* from several studies are shown in Fig. 4.4. The earlier studies of age and growth of *Squalus acanthias*, which were not validated, probably underestimated age by rejecting some bands (McFarlane and Beamish, 1987b). Holden and Meadows (1962) and Nammack *et al.* (1985) rejected certain bands, which they did not consider to be annual. Ketchen (1975) rejected spines where counts were in disagreement by more than ± 2 years. The McFarlane and Beamish (1987b) validation study showed that *Squalus acanthias* in the Strait of Georgia (one of Ketchen's study areas) were much longer lived than previously thought. Underestimation of age will result in assumptions that a species reaches asymptotic length more rapidly than in reality. A direct comparison of the study McFarlane and Beamish in the Pacific and that of Holden and Meadows (1962) in the North Sea or Nammack *et al.* off the eastern US, may be dangerous, in view of the wide separation of the areas. However it is likely that these authors, in rejecting certain annuli, underestimated age in this species. In the present study no bands were considered to be sub-annual and under-estimation of age is considered to be unlikely. Consequently, predictions of yield based on these estimates can be considered conservative.

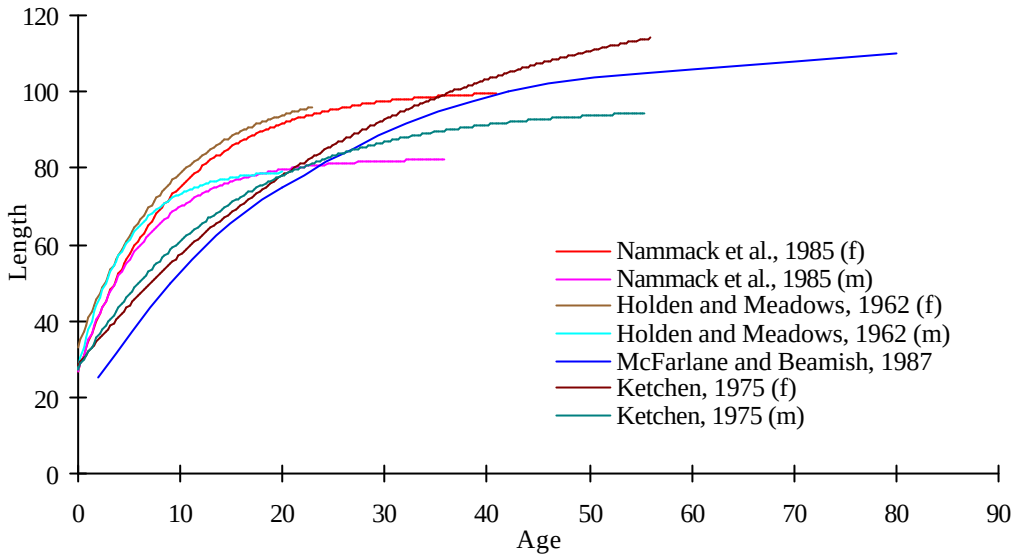

Fig. 4.4. Comparison of growth curves for *Squalus acanthias* from the literature. The studies are those of Holden and Meadows (1962) for the North Sea, Ketchen (1975) for the Strait of Georgia, NE Pacific, Nammack *et al*. (1985) for the eastern US and McFarlane and Beamish (1987) Strait of Georgia, NE Pacific.

Underestimation of age will result in overestimation of growth rate (Beamish and McFarlane, 1983) and has the effect of producing artificially high values of the von Bertalanffy parameter K. Maximum yield in analysis of yield studies is reached at a greater fishing mortality (F) for stocks with higher values of K than those with lower values (King, 1995). As noted by Beamish and McFarlane (1983) underestimation of age of sablefish *Sebastes alutus* led to assumptions about the state of the stock that produced erroneous stock predictions. Subsequent analysis, based on validated ages indicated that the stock had been reduced to about 18 % of initial biomass (Archibald *et al.*, 1983). The estimate of F in the present study represents the most up to date possible. Yield per recruit models suggest that species with high growth rates, and high values of K require greater levels of fishing mortality F to obtain maximum yield (King, 1995) and by inference, slower growing species such as *Deania calceus* will reach maximum yield at relatively smaller value of F.

The General Principles and Article 6.5 of the UN Food and Agriculture Organisation (FAO) International Code of Conduct for Responsible Fisheries prescribes a "Precautionary Approach to all fisheries regardless of their jurisdictional nature recognising that most problems affecting the sector result from insufficient precautions in management regimes when faced with a high level of uncertainty." The International Council for the Exploration of the Sea (ICES) developed a series of precautionary reference points to allow for management of fish stocks in line with the Precautionary Approach. In the case of deepwater species where there is little available biological data ICES holds that precautionary approach values of fishing mortality (F_{pa}) be set as equal to M (Anon, 2000b). Estimates of current F slightly exceed M for *Deania calceus*. Therefore in accordance with the Precautionary Approach fishing mortality should remain at these levels. In the case of male *Deania calceus* F is below M. Therefore some increase in fishing effort on males may be possible within "precautionary approach" reference points. Notwithstanding the fact that males predominate in catches of this species at all depths and on all surveys it may not be possible to select for males over females. While it is not clear to what extent vessels fish in the depths where *Deania calceus* is most abundant, further fishing pressure on this species may be counter-productive. In the case of *Centrophorus squamosus* estimated M is very low. In order

to maintain fishing effort within the requirements of the FAO precautionary approach to fisheries management F will have to be kept at very low levels also.

4.9 The impacts of fishing

In the northeast Atlantic, sharks are mainly taken in the mixed-species trawl fishery by French (Charuau *et al*., 1995) and more recently by Scottish (Gordon, 1999) vessels. Sharks are also caught on long-line (Iglesias and Paz, 1995; Pineiro *et al*., 1998). The results of this study support Gordon's (1999) suggestion that deepwater long-line fisheries are not selective for sharks, and in addition, discards are high. There is evidence from this study that sharks, especially *Deania calceus*, can escape trawls. Long-lines are a more efficient means of catching sharks than trawls and the species under study comprise a larger proportion of long-line catches (Connolly and Kelly, 1996). Increased fishing by long-liners may impact on shark populations. It should be emphasised that since the smallest sharks are absent from the fishing grounds they are not within the range of the fishery. The geographical range of the stocks is unknown. However countries are investigating new deepwater fishing grounds at Hatton, Lousey and Lorien Banks, the Mid Atlantic Ridge and the western slopes of the Rockall Bank (Duran *et al*., 2000; Langedal and Hareide, 2000; Vinnichenko, 2000). This increased effort, while sustaining landings, will extend the range of exploitation. CPUE may not offer a means to identify trends in abundance in these expanding fisheries.

It has often been stated that elasmobranchs cannot sustain high levels of fishing pressure because of their characteristic slow growth, longevity and low fecundity (Bonfil, 1994; Hoenig and Gruber, 1990; Holden, 1973). However Stevens *et al*. (1996) pointed out that not all elasmobranchs are slow growing and have low productive capacities.. Walker (1998) considered that more productive sharks could sustain greater fishing pressures than less productive species. But the present study has shown that these deepwater sharks have life history parameters that indicate they are among the less productive elasmobranchs. These findings support the view that deepwater fish fauna are slow growing, have low fecundities and are susceptible to overexploitation (Gordon *et al*., 1995a; Merrett and Haedrich, 1997). Multi-species fisheries, with a shark by-catch will lead to the depletion of elasmobranchs unless steps are taken to mitigate by-catch

(Stevens *et al.*, 1996). The fisheries in which deepwater sharks are taken in the northeast Atlantic are multi-species in character (Charuau *et al*., 1995; Pineiro *et al*., 1998) and it does not seem possible that shark by-catch can be regulated. While single species elasmobranch fisheries may be managed in a sustainable way, as outlined by Walker (1998) it will be difficult to achieve this goal for the mixed-species deepwater shark fishery. The multi-species nature of the fishery and the life-history characteristics of the target and by-catch species are difficult to reconcile with sustainable management.

In view of their life-history strategies, recovery of deepwater species from heavy fishing pressures will be slow (Gordon *et al*., 1995a). Apparent density-dependent changes in fecundity, due to exploitation, have been described for shelf-dwelling elasmobranchs (Gauld, 1979). It is not clear whether the greater fecundity and lower size at maturity of *Centroscymnus coelolepis* in Suruga Bay, Japan, is a density-dependent response to exploitation, or a natural feature of the population. Whether or not the species under study are capable of density-dependent responses, it is likely that such changes will be slower than for *Squalus acanthias*. Whilst their fecundites are similar to that of *Squalus acanthias* (Hanchet, 1988; Holden and Meadows, 1964) they differ by not developing subsequent batches of ova during gestation. If these species are capable of density dependent increases in fecundity the length of the reproductive cycle will mean that such response times will be even longer than for *Squalus acanthias*, which has been shown to be susceptible to over-exploitation (Fahy, 1992; Ketchen, 1986).

Stevens *et al*. (2000) used ecosystem modelling to investigate the effects of the removal of sharks on shelf ecosystems but surmised that the effects of such depletion are "complex and fairly unpredictable". Several authors have documented changes in the species composition of shelf waters, due to the selective removal of predators. The increased abundance of small rays in the Irish Sea has been attributed to the availability of food as larger rays declined (Dulvy *et al*., 2000). Furthermore increased abundance of dogfish in the northwest Atlantic has been attributed to declines in gadoids, since they have over-lapping prey preferences (Murawski and Idoine, 1994). No such studies have been conducted in deep waters to date, but Gordon *et al*. (1995a) stated that since deepwater fish are slow growing, population regeneration and recovery from the effects of the disturbance of fishing will be very slow. These authors go on to suggest that the

overall community impact of such disturbance could not be predicted. Merrett and Haedrich (1997) and Clark *et al*. (2000) suggest that there is no evidence of compensatory replacement by new deepwater predators. Haedrich and Barnes (1997) described declines in size in deepwater fish community in the northwest Atlantic (Haedrich and Barnes, 1997). Reflecting on these changes, Merrett and Haedrich (1997) state that fishing pressures favour smaller fish. They go on to propose that the entire ecosystem might stabilise at a new steady state, favouring increased abundance of faster-growing, smaller fish species that could take advantage of the excess food resources available.

4.10 Management of the fishery

Fishing is analogous to the introduction of a new predator at the summit of the deepwater food web (Merrett and Haedrich, 1997). Many fisheries have evolved by targeting progressively lower trophic levels (Pauly *et al.*, 1998). However since deepwater food webs are largely dependent on allochthonous production (Mauchline and Gordon, 1991; Gordon *et al*., 1995a) this strategy is not possible. Turnover times of deepwater species are long. Therefore the only possible strategy for deepwater fishing vessels is to search out new prey, deplete them and move on again - an approach more akin to mining than harvesting (Merrett and Haedrich, 1997). The orange roughy fishery off New Zealand has conformed to this pattern, with reduced biomass and a rapid contraction in distribution to seamounts and isolated areas (Clark *et al.*, 2000). A similar trend appears to be taking place in the northeast Atlantic at present; as CPUE declines on the continental slope grounds, new fisheries on offshore banks and seamounts are being developed - as evidenced by information made available to ICES (Anon., 2000b). Bridger's (1978) statement, that the profitability of deepwater fishing would depend on markets being secured for the sharks, could equally be applied to these new fisheries. Indeed, the hitherto non-commercial black dogfish *Centroscyllium fabricii* is now being landed by French trawlers (Lorrance and Lespagnol, 2000).

At present there are no explicit management objectives for deepwater sharks, or indeed any elasmobranch species, in the northeast Atlantic (Pawson and Vince, 1999). Yet the FAO International Code of Conduct for Responsible Fisheries requires that countries

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manage fish stocks regardless of whether scientific data are available or not (FAO, 1996). While only three countries, the USA, Australia and New Zealand currently have shark management regimes in place (Walker, 1998), the FAO has recommended that all states should adopt a national plan of action for conservation and management of shark stocks (FAO, 1998b). In the northeast Atlantic fisheries management is based on the scientific advice provided by ICES, but to date, no regular stock assessments have been carried out because of the lack of data (Pawson and Vince, 1999). Recently, the Commission of the European Communities has recently funded an international programme to develop stock assessments for elasmobranchs, including *Centrophorus squamosus* and *Centroscymnus coelolepis*. This project will improve the quality of existing information and adapt assessment methods to the data available (Anon., 1999).

Data for stock assessments are slowly becoming available, while the fisheries are developing and diversifying rapidly (Merrett and Haedrich, 1997). In view of the FAO precautionary approach to fisheries (FAO, 1996) and voluntary shark management initiative (FAO, 1998b) it is clear that there is need for a management programme for deepwater shark fisheries. Such a management regime will require adequate scientific data. The first deepwater shark assessment was carried out by ICES in 2000, using production and depletion models based on CPUE from French vessels for *Centroscymnus coelolepis* and *Centrophorus squamosus* combined (Anon., 2000b). While this is the only CPUE information available it does not offer a clear reflection of biomass trends for either species. Anderson (1990) noted that many attempts to assess elasmobranch stocks have suffered from insufficient data or the use of inappropriate models. In one of the most comprehensive shark assessment studies Rago *et al*. (1998) recommended that greater dependence should be placed on approaches that incorporate known information about the life history parameters of the species under study. These authors used age, growth and reproductive information as inputs to a life-table, estimating the number of pups per female recruit. This approach identified the level of fishing mortality that the stock could sustain without going into decline. Such an approach seems applicable to deepwater squalids, since much life-history information is now available.

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Appendix I Data Sheets

DEEP WATER SAMPLING CRUISE

DATE | STATION | AREA

	POSITION	TIME	DEPTH	WARP
SHOOT				
HAUL				

TOW SPEED

	Grenadier	Redfish	Scabbard	forkbeard	Coelolepis	Squamosus	Daenia	Others	Discards	TOTAL
No. BOXES										
No. SAMPLED										

BOTTOM TYPE | WEATHER

COMMENTS

DATE | STATION | AREA | FACTOR

Wt OF UNSORTED CATCH | Wt OF CATCH SUBSAMPLED

SPECIES	S	M	O	SEX	MAT	ST.	GO.	TOT kg	SAMPkg	NOTES
ARGENTINES										
Argentina silus										
SMOOTHHEADS										
Alepocephalus bairdi										
REDFISH										
Helicolenus dactylopterus										
Sebastes mentella										
Scorpaena cristulata echinata										
Sebastes viviparous										
RABBITFISH										
Chimera monstrosa										
Hydrolagus miriablis										
SCABBARDS										
Aphanopus carbo										
GRENADIERS										
Coelorhyncus coelorhyncus										
Coryphaenoides rupestris										
Macrourus berglax										
Trachyrhyncus murrayi										
Trachyrhyncus scabrus										
ORANGE ROUGHY										
Hoplostethus atlanticus										
Hoplostethus mediterraneus										
COD LIKE FISH										
Brosme brosme										
Molva dypterygia										
Mora moro										
Phycis blennoides										
FLATFISH										
Reinhardtius hippoglossoides										
Lepidorhombus whiffiagonus										
SHARKS										
Apristurus										
Centrophorus squamosus										
Centroscymnus coelolepis										
Centroscymnus crepidater										
Deania calceus										
Etmopterus spinax										
Etmopterus princeps										
Galeus melastomus										
RAYS										
Breviraja cerulea										
Raja bathyphila										
Raja fyllae										
Raja nidarosiensis										
Raja oxyrhyncus										
Discards										

DATE		STATION		AREA	
SPECIES		CATCH WT.		SAMPLE WT.	

No.	Len	Wt.	sex	mat.	st.	Age	Gon.		No.	Len	Wt.	sex	mat.	st.	Age	Gon.	
1									51								
2									52								
3									53								
4									54								
5									55								
6									56								
7									57								
8									58								
9									59								
10									60								
11									61								
12									62								
13									63								
14									64								
15									65								
16									66								
17									67								
18									68								
19									69								
20									70								
21									71								
22									72								
23									73								
24									74								
25									75								
26									76								
27									77								
28									78								
29									79								
30									80								
31									81								
32									82								
33									83								
34									84								
35									85								
36									86								
37									87								
38									88								
39									89								
40									90								
41									91								
42									92								
43									93								
44									94								
45									95								
46									96								
47									97								
48									98								
49									99								
50									100								

Marine Fisheries Services Division
Deepwater Long-line Survey

DATE	STATION	AREA

SHOOT	BEGIN	END
TIME		
DEPTH		
LATITUDE		
LONGITUDE		
NUMBER OF MAGAZINES		
LINE (mm)		
No. of HOOKS		

HAUL	BEGIN	END
TIME		
DEPTH		
LATITUDE		
LONGITUDE		
NUMBER OF MAGAZINES		
LINE (mm)		
No. of HOOKS		

WEATHER	BOTTOM

PROFILE OF SEA BED	metres

COMMENTS

Species Sheet **Deepwater Long-line Survey**

DATE	AREA	STATION

SPECIES	Length	Sex / Maturity	Weight	Biological	Notes
Sharks					
Centrophorus squamosus					
Centroscymnus coelolepis					
Deania calcea					
Centroscymnus crepidater					
Etmopterus spinax					
Etmopterus princeps					
Dalatias licha					
Apristurus laursonii					
Apristurus aphyodes					
Apristurus manis					
Galeus melastomus					
Galeus murinus					
Rays					
Raja fyllae					
Raja bathyfyllae					
Raja fullonica					
Raja circularis					
Raja kukujevi					
Bathyraja richardsoni					
Rabbitfish					
Chimaera monstrosa					
Gadoids					
Mora moro					
Lepidion eques					
Antimora rostrata					
Brosme brosme					
Molva molva					
Molva dypterygia					
Phycis blennoides					
Others					
Synaphobranchus kaupi					
Reinhardtius hippoglossoides					
Sebastes marinus					
Sebastes mentella					
Sebastes viviparous					
Helicolenus dactylopterus					

SPECIES | AREA | catch wt.

STATION | sample wt.

DATE

Number	Length	Round Weight	Sex	Maturity	Liver Wt.	Tsts/utrs wd. L	Tsts/utrs wd. R	Wd. L Shell G.	Wd. R Shell G.	Egg No. L/R	D. Lrgst egg L.	No. Lrgst egg L/R	D. Lrgst egg R.	D. next l. egg L.	No. nxt l. egg L/R	D. next l. egg R.	Embryo No. L/R	Gonad Wt.	Gutted Wt.
1																			
2																			
3																			
4																			
5																			
6																			
7																			
8																			
9																			
0																			
1																			
2																			
3																			
4																			
5																			
6																			
7																			
8																			
9																			

Elasmobranch Length Frequency Sheet

Deepwater Long line Survey MFV:

Date **Haul** **Sampler**

Species:						Species:					
Weight						Weight					
Len	male	Tot.	Len	female	Tot.	Len	male	Tot.	Len	female	Tot.
0			0			0			0		
1			1			1			1		
2			2			2			2		
3			3			3			3		
4			4			4			4		
5			5			5			5		
6			6			6			6		
7			7			7			7		
8			8			8			8		
9			9			9			9		
0			0			0			0		
1			1			1			1		
2			2			2			2		
3			3			3			3		
4			4			4			4		
5			5			5			5		
6			6			6			6		
7			7			7			7		
8			8			8			8		
9			9			9			9		
0			0			0			0		
1			1			1			1		
2			2			2			2		
3			3			3			3		
4			4			4			4		
5			5			5			5		
6			6			6			6		
7			7			7			7		
8			8			8			8		
9			9			9			9		
0			0			0			0		
1			1			1			1		
2			2			2			2		
3			3			3			3		
4			4			4			4		
5			5			5			5		
6			6			6			6		
7			7			7			7		
8			8			8			8		
9			9			9			9		
0			0			0			0		
1			1			1			1		
2			2			2			2		
3			3			3			3		
4			4			4			4		
5			5			5			5		
6			6			6			6		
7			7			7			7		
8			8			8			8		
9			9			9			9		
0			0			0			0		
1			1			1			1		
2			2			2			2		
3			3			3			3		
4			4			4			4		
5			5			5			5		
6			6			6			6		
7			7			7			7		
8			8			8			8		
9			9			9			9		

Appendix II Details of Fishing Gears

Trawl

Door Type:	Polyice
Door Weight:	1,800 kg
Single Bridles	50 fathoms
Double Bridles	25 fathoms
Towing Speed:	2.3 – 3.2 knots
Cod-end liner:	25 mm knot to knot
Net Type:	Deepwater Trawl
Net Manufacturer:	Gundry's Ltd., Killybegs, Ireland
Mesh size:	105 mm knot to knot
Footrope:	36 m of 14 mm grade 80 chain
Bobbins:	16 inch
Floats:	180 x 8 inch
Headline Height:	3.6 – 5 m
Door Spread:	24 – 27 m

Long-line

Main line:	9mm and 11 mm
Hook Manufacturer:	Mustad, Gjovik, Norway
Hook Type:	EZ
Hook Size:	13/0 and 7/0 EZ
Snood length:	40 – 70 cm
Interval between swivels:	1.4 m
Interval between anchor and 1st swivel:	100 fathoms
Anchor:	30 – 50 kg at each end of main line
Weight on buoy line:	35 – 40 kg chain
Interval between chain and anchor:	3 – 4 fathoms
Dahn:	Reflector buoy x 3
No. hooks per magazine:	1,350
Bait:	squid 60 %, mackerel 40 %

Appendix III Maturity Scale

MATURITY SCALE E 2

Aplacental and placental viviparous sharks

(by M. Stehmann, ISH - March 1998)

MALES *

A or **1** = **immature, juvenile**

Claspers undeveloped as small, flexible sticks being shorter than extreme tips of posterior pelvic fin lobes. Gonads (testes) small, whitish, sperm ducts straight and thread-like.

B or **2** = **maturing, adolescent, subadult**

Claspers becoming extended, longer than tips of posterior pelvic fin lobes, their tips (glans) becoming structured, but their skeleton still soft and flexible. Gonads enlarged, sperm ducts beginning to meander posteriorly.

C or **3** = **mature, adult**

Claspers fully formed and stiff, eventually present cartilaginous hooks, claws or spines of glans free and sharp. Gonads enlarged, well rounded, filled with flowing sperm and often reddish in colour. Sperm ducts tightly coiled and well filled with sperm.

D or **4** = **active**

Glans clasper often dilated and swollen, with free cartilaginous spine mostly erect; sperm flowing from cloaca under pressure on seminal vesicle and/or present in clasper groove.

FEMALES - ovarian stages

A or **1** = **immature, juvenile**

Ovaries small, their internal structure gelatinous or granulated. No oocytes differentiated or all uniformly small, granular. Oviducts (uteri) narrow, thread-like.

B or **2** = **maturing, adolescent**

Ovaries somewhat enlarged, walls more transparent. Oocytes becoming differentiated to various small sizes. Uteri largely as stage A/1 but may become widened posteriorly.

C or **3** = **mature, adult**

Ovaries large, well rounded. Oocytes obviously enlarged, all to about the same size, can easily be counted and measured.

FEMALES - uterine stages

D or **4** = **developing**

Uteri well filled and rounded with seemingly unsegmented yolk content („candle")

E or **5** = **differentiating**

Uteri well filled and rounded with segmented content of large yolk balls, can easily be counted and measured. Embryos variously small, atop their huge yolk balls, larger ones with external gills and unpigmented (still „candle").

F or **6** = **expecting**

Embryos more or less fully formed, pigmented, external gills lost, yolk sacs obviously reduced. Can be counted, measured and sexed easily.

G or **7** = **post-natal, spent**

Ovaries at resting stage, similar to stages A/1 or B/2. Uteri empty but still widened considerably over their full length in contrast to stages A/1 or B/2.

* Stages 3 and 4 were combined for males.

Appendix IV Explanation of Statistical Terms

Allometric Growth Curves

The allometric regression of the form;

$\mathbf{Y = aX^b}$

is often transformed by natural logarithms to the linear equation;

Log Y = log a + b * log X

This is widely applied to organisms where the ratio between increments in structures of different size remains roughly constant, yielding a relatively greater increase in one variable with respect to the other on a linear scale (Sokal and Rohlf, 1995).

The above equations can be used to describe the relationship between length and weight in fish, thus;

$\mathbf{W = aL^b}$**,**

or

Log W = log a + b * log L

Where the b exponent of these equations equals 3, the equations describe "isometric growth" in weight, where a fish has an unchanging body form and relative density (Ricker, 1975). However, where b does not equal 3, a condition referred to as allometry obtains. In the case of linear measurements isometric growth is characterised by a b exponent of 1. A value of less than 1 is referred to as negative allometry and describes a condition where the parameter in question grows smaller, relative to the total body size parameter (Simpson *et al.*, 1960).

Ricker (1973; 1975) recommends that Geometric Mean (G.M.) functional regression, the Model II regression of Sokal and Rohlf (1995), is a more appropriate means by which to carry out weight length regression than the

ordinary least squares method. Model II regression minimises the products of the distances of both x and y coordinates from the predicted regression line, a compromise is reached between least squared deviates of both x and y. However Ricker does not present any means by which to test for significant differences in 2 or more regressions. Furthermore ANCOVA is based on Model I regression (Sokal and Rohlf, 1995). These authors could not recommend that ANCOVA be used with Model II regressions until analysis of covariance techniques are developed for this type of model. In the present study, Model I regression was used in the absence of any adequate statistical tests for Model II techniques.

The regression coefficient for y on x by ordinary least squares (Model I) regression is

$$\mathbf{b} = \frac{\mathbf{S\,xy}}{\mathbf{S\,x^2}}$$

and the regression coefficient for GM functional (Model II) regression of y on x is

$$\mathbf{v} = \text{Ö}\ \frac{\mathbf{S\,y2}}{\mathbf{S\,x2}}$$

Gabriel's Approximate Method

In order compare a set of regression coefficients it is convenient to make use of Gabriel's Approximate Method in which "comparison intervals" are constructed such that two regression coefficients are significantly different if and only if their intervals do not overlap. Hochberg's GT2 method yielded the narrower intervals (Sokal and Rohlf, 1995).

$$L_i = b_i - \sqrt{0.5} * m_{a[k^*,?]} S_{bi}$$

$$L_u = b_i + \sqrt{0.5} * m_{a[k^*,?]} S_{bi}$$

Where

L_i = lower bound of comparison interval

L_u = upper bound of comparison interval

b_i = regression coefficient (slope)

a = significance level

k* = number of comparisons (between slopes) †

m = critical value of the studentised maximum modulus distribution

S_{bi} = standard error of slope †

†Where Gabriel's approximate method was used for comparisons of k* intercepts the standard error of the mean of that regression S_{Yi}, adjusted for the mean value of the covariate was substituted for S_{bi}.

Appendix V Protocol for Wax Infiltration

1.	4 % Buffered Formalin	1 hour	35 ^{0}C	
2.	70 % Alcohol	1 hour	35 ^{0}C	P
3.	90 % Alcohol	30 minutes	35 ^{0}C	P
4.	95 % Alcohol	30 minutes	35 ^{0}C	P
5.	95 % Alcohol	30 minutes	35 ^{0}C	P
6.	100 % Alcohol	45 minutes	35 ^{0}C	P
7.	100 % Alcohol	1 hour	35 ^{0}C	P
8.	Xylene	1 hour	35 ^{0}C	P
9.	Xylene	1 hour	35 ^{0}C	P
10.	Xylene	1 hour	35 ^{0}C	P
11.	Wax	30 minutes	60 ^{0}C	P
12.	Wax	30 minutes	60 ^{0}C	P
13.	Wax	30 minutes	60 ^{0}C	P
14.	Wax	30 minutes	60 ^{0}C	P

P indicates that pressure/vacuum cycle was employed

Appendix VI Protocol for Staining of Slides

1.	Xylene	2 minutes
2.	Xylene	2 minutes
3.	Absolute Alcohol	1 minute
4.	95 % Alcohol	1 minute
5.	70 % alcohol	1 minute
6.	Water	2 minutes
7.	Haematoxylin	1 minute 40 seconds
8.	Water	2 minutes
9.	0.25 % Acid Alcohol	40 seconds
10.	Scott's Tap Water	50 seconds
11.	Water	2 minutes
12.	Eosin	35 seconds
13.	70 % Alcohol	25 seconds
14.	95 % Alcohol	25 seconds
15.	Absolute Alcohol	55 secnds
16.	Xylene	2 minutes
17.	Xylene	2 minutes
18.	Xylene	2 minutes
19.	Xylene	2 minutes
20.	Cover slips	
21.	Fume cupboard	overnight

Appendix VII Publications associated with this work

Clarke, M.W., Connolly, P.L. and Bracken, J.J. 2001. Aspects of reproduction of the deepwater sharks *Centroscymnus coelolepis* and *Centrophorus squamosus* from west of Ireland and Scotland. *Journal of the Marine Biological Association of the United Kingdom.*. 81: 1019-1029.

Clarke, M.W., Connolly, P.L. and Bracken, J.J. 2002a. Age estimation of the exploited deepwater shark *Centrophorus squamosus* from the continental slopes of the Rockall Trough and Porcupine Bank. *Journal of Fish Biology*, 60: 501-514.

Clarke, M.W., Connolly, P.L. and Bracken, J.J. 2002b. Catch, discarding, age estimation, growth and maturity of the squalid shark *Deania calceus* west and north of Ireland. *Fisheries Research* 56: 139-153.

Publications associated with the Marine Institute Deepwater Programme

Clarke, M. W. 2000. Records of deepwater chondrichthyan fish caught on long-line in the Rockall Trough. *Journal of the Marine Biological Association of the U.K.*, **80**, 377-378.

Clarke, M., Connolly, P. L., and Bracken, J. J. 1998. Age estimation of the squaliform shark *Centrophorus squamosus* (Bonnaterre, 1788) using the second dorsal spine. *ICES CM* 1998/ **0: 41**.

Clarke, M. W., Connolly, P. L., and Kelly, C. J. 1999. Preliminary Catch, Discards and Selectivity Results of Trawl Survey on Deepwater Slopes of the Rockall Trough. Dublin: Marine Institute. Fisheries Leaflet no. 178.

Connolly, P. L., Kelly, C. J., and Clarke, M. W. 1999. Long-line Survey of the eastern slopes of the Rockall Trough. Dublin: Marine Institute. Fisheries Leaflet no. 200.

Kelly, C. J., Clarke, M., and Connolly, P. L. 1997. Catch and discards from a deep water trawl survey in 1996. Dublin: Marine Institute. Fisheries Leaflet no. 175.

Kelly, C. J., Connolly, P. L., and Clarke, M. W. 1998. The deep water fisheries of the Rockall trough; some insights gleaned from Irish survey data. *ICES CM* **1998/O:40.**